For Reference

NOT TO BE TAKEN FROM THIS ROOM

For Reference

NOT TO BE TAKEN FROM THIS ROOM

Ex libris
universitatis
albertaensis

University of Alberta

Digitized by the Internet Archive
in 2019 with funding from
University of Alberta Libraries

https://archive.org/details/cowcalfrelations00pene

FRONTISPIECE

Bison cow with calf suckling.

esis
1963
43

THE UNIVERSITY OF ALBERTA

THE COW-CALF RELATIONSHIP AND RUTTING BEHAVIOR IN THE AMERICAN BISON

by

PENELOPE JANE MARJORIBANKS EGERTON

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

NOVEMBER 1962

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled The Cow-calf Relationship and Rutting Behavior in the American Bison submitted by Penelope J. Marjoribanks Egerton in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

The social behavior of American bison was studied in a confined herd in Waterton Lakes National Park and in wild herds in Wood Buffalo National Park. Particular aspects of the study were calf behavior, the social integration of calves and rutting behavior. General activity in the herds was rhythmical, with periods of grazing alternating with those of resting. An almost linear dominance hierarchy existed in the Waterton herd. Interactions were more frequent between animals close in rank than between those farther apart. Bulls dominated cows in the same age group.

Data on calf behavior and the cow-calf relationship were based on observation of the seven calves in the Waterton herd. Cows left the herd at parturition, and remained away for some time afterwards. Probably the period when a cow and her calf are alone, is important in the formation of a bond between them. Udder-seeking behavior in newborn ungulates is discussed. At first, cows prevented contact between their calves and other herd members. Success in this depended upon the cow's rank in the hierarchy. Calves began to play with other calves when about a week old. Play included chasing, fighting and mounting. The significance of play is discussed. Suckling behavior is described. Calves sometimes stopped their mothers moving, or induced them to stand, and then suckled. Social integration of calves involved gradually increasing independence of calves from their mothers,

and developmemt of the calves' behavior to resemble that of adults.

In Wood Buffalo Park during the rut, most bison were in small herds containing members of both sexes, including about three adult bulls. There were also many lone bulls. Behavior within the herds and interactions between members of the herds and lone bulls are described and discussed. Lone bulls played an important role in the rut. Bulls less than five years old probably do not breed in the wild state. Fighting occurred only between bulls of different herds, not within herds. The tending bond functions as courtship behavior between a cow and bull. Under natural conditions, rutting behavior is a process resulting from the interaction of behavior occurring within herds and that occurring between herds.

ACKNOWLEDGEMENTS

I am very grateful to Dr. S. A. Altmann for his help and interest throughout the study, and for help in interpretation of data; and to Dr. W. A. Fuller for encourageing the undertaking of the project and for his helpful suggestions on reading the manuscript.

I should like to thank the following people, whose interest and cooperation made the field work possible: F. Camp, Chief Warden, and R. W. Thompson, Warden, Waterton Lakes National Park; B. E. Olson, Superintendent and K. F. Cooper, Wood Buffalo National Park; H. R. Webster, Superintendent, and W. D. Armstrong, Warden, Elk Island National Park. Mrs. R. W. Thompson and Mrs. K. F. Cooper showed me every kindness, in making me welcome in their homes during summer 1961.

The project was financed by a teaching assistantship and a general research grant from the University of Alberta, and by a bursary from the National Research Council of Canada. Travel to Wood Buffalo National Park was financed by the Canadian Wildlife Service.

TABLE OF CONTENTS

PAGE

LIST OF TABLES vi

LIST OF FIGURES vii

INTRODUCTION 1

METHODS 3

BACKGROUND INFORMATION 4

History of the bison studied 4
Habitat of the Waterton bison 4
Composition of the Waterton herd 6
General activity of the herd 8
Effects of weather on behavior 14
Description of certain behavior patterns 14

THE DOMINANCE HIERARCHY 17

Introduction 17
Methods 18
Threat behavior 19
Passive displacement 21
Results 23
Discussion 26
The significance of dominance 36

THE BEHAVIOR OF CALVES AND THE RELATIONSHIP BETWEEN COW AND CALF 38

Introduction 38
The calving season 38
Appearance of the pregnant cow 39
The process of parturition 42
Behavior of the cow and its newborn calf 44
First contact of calf with other bison 47
Discussion 49
Udder-seeking behavior 49
Behavior of the cow at parturition 52
Behavior of the cow and calf after rejoining the herd... 52
The cow-calf subgroup 52
Activity of the cow and calf 53
Play 57
The nature of play 57
Solitary play in calves 58
Play between calves 60
Invitation to play.................................... 61
Play-fighting in calves 62
Mounting behavior 65
The significance of play 67

TABLE OF CONTENTS (cont.) PAGE

Vocal communication between cow and calf 71
Differences in behavior between calves and adults 75
Suckling behavior 81
    Occurrence 81
    Duration of suckling 82
    Position of the calf while suckling 84
    "Heading-off" 86
    Calves inducing their mothers to stand 87
    Variations in suckling behavior 90
    Weaning 91

DISCUSSION 94

The social integration of the bison calf 94

THE RUT IN BISON 99

Introduction 99
The rutting season 100
The herd structure in Wood Buffalo Park 101

RUTTING BEHAVIOR 108

Occurrence of rutting behavior 108
Characteristics of the rut in the Waterton bison 109
Rutting behavior in Wood Buffalo Park 110
    The lip-curl posture 111
    The tending bond 115
    Age of tending bulls 117
    Atypical tending bonds 119
Inter-herd behavior 120
    Interactions with lone bulls 120
    Interactions between herds 124
    The effect of the rut on calves of the year. 128

DISCUSSION 135

The role of different bulls during the rut 135
Fighting behavior and the significance of pawing, horning and wallowing in bulls 137
The significance of the tending bond 140
Differences in rutting behavior between bison in Waterton Park and Wood Buffalo Park 143

SUMMARY 145

LITERATURE CITED 151

LIST OF TABLES

PAGE

Table I. Composition of the Waterton herd. 5

Table II. Data on Parturition. 43

Table III. Play-fighting in calves. 63

Table IV. Mounting behavior in calves. 66

Table V. Lip-curling behavior in calves. 79

Table VI. Duration of suckling. 83

Table VII. Calves inducing their mothers to stand. 89

Table VIII. Average composition of 35 mixed herds in Wood Buffalo Park. 104

LIST OF FIGURES

PAGE

Frontispiece. Bison cow with calf suckling.

Fig. 1. Waterton herd during evening activity period. 9

Fig. 2. Waterton herd during a resting period. 10

Fig. 3. Waterton herd drinking at a lake. 11

Fig. 4. Aggression over a hay bale. 20

Fig. 5. Fighting over salt. 22

Fig. 6. The Dominance hierarchy in the Waterton herd. 24

Fig. 7. Total observed and theoretical interactions for bison of proximity number 1-31. 30

Fig. 8. Diagram explaining calculations in Fig. 7. 32

Fig. 9. Total observed and theoretical interactions for bison of proximity number 8-31. 34

Fig. 10. Appearance of pregnant bison cow. 40

Fig. 11. Grazing pattern of cow around her newborn calf. 54

Fig. 12. Cow lying while its calf suckles. 85

Fig. 13. Calf butting its mother. 88

Fig. 14. Number of bison in each of 48 mixed herds, Wood Buffalo Park. 103

Fig. 15. Number of adult bulls in each of 35 mixed herds, Wood Buffalo Park. 106

Fig. 16. The Lip-curl posture. 112

Fig. 17. Bull sniffing genital region of cow. 113

Fig. 18. Bull horns ground. 122

LIST OF FIGURES (cont.).

PAGE

Fig. 19. Fighting behavior: two bulls approach one another. 130

Fig. 20. Fighting behavior: two bulls stand facing one another. 131

Fig. 21. Fighting behavior: two bulls fighting. 132

Fig. 22. Fighting behavior: a pause in the fight. 133

Fig. 23. Fighting behavior: close-up of two bulls fighting. 134

INTRODUCTION

The extensive literature on the history of the North American bison (Bison b. bison), contains numerous references to the behavior of this species. Many of these references are generalizations based on few actual observations, or on second-hand information, and their accuracy is often open to doubt.

Two recent works, however, those of Fuller (1960) and McHugh (1958), deal in detail with the behavior of the bison. These are the most complete works on the subject. One aspect of bison behavior that was not studied in any detail by Fuller or McHugh, however, is that of the behavior of calves, and the relationship between cow and calf.

The main purpose of my study was to obtain information on these subjects, and on the development of the behavior of calves as they grow older. The second object of my study was to get information on the rutting behavior of bison, knowledge of which is also limited. Observations were also made on the social structure of a herd of bison, and on the general activity of the herd.

My study was carried out from 3 May to 15 September 1961. Most of the work was done with a captive herd in Waterton Lakes National Park, Alberta, between 3 May and 14 August. From 20 August to 15 September, observations were made on the free-ranging bison in Wood Buffalo National Park. Other data were obtained in Elk Island National Park, during

the round-up in November 1961.

The work on herd activity, the social structure of the herd, and the behavior of calves was done in Waterton Park. I thought it preferable to do the study on rutting behavior on wild, free-ranging bison in Wood Buffalo Park, because I thought that the fixed herd composition and the confinement of the Waterton herd might alter natural rutting behavior. Another purpose in working in Wood Buffalo Park was to see to what extent the general behavior of the Waterton bison was altered by the confinement of the herd.

METHODS

While in Waterton Park I stayed with the family of Warden R. W. Thompson. I used either a bicycle or one of the park horses to go each day to the bison paddock, three miles away. In Wood Buffalo Park I stayed with Mr. and Mrs. K. F. Cooper at the Buffalo Management Camp, Sweetgrass. K. F. Cooper is the superintendent of this camp, and, having lived in the area for several years, he has considerable knowledge of bison. He gave me certain information referred to later.

In Wood Buffalo Park, most observations were made from horseback, partly because the bison were easier to approach on horseback than on foot, and partly because the grass on the meadows was so long that when on foot I could not see the bison if they were more than a few yards away.

Throughout the study, I used Zeiss 10 x 50 binoculars, and made field notes on data sheets or in a note book at the time of observation. I took color and black and white 35 mm. photographs, and with the assistance of R. W. Thompson, in Waterton Park, I also took 1000 feet of 16 mm. color motion picture film, to illustrate the behavior of the bison.

BACKGROUND INFORMATION

History of the Bison in Wood Buffalo Park and Waterton Park

Fuller (1962) has given an account of the history of the bison in Wood Buffalo Park. The bison there now are the descendants of about 1500 wood bison (*Bison b. athabascae*) that remained in 1922 and of 6,673 plains bison (*Bison b. bison*) that were shipped from Wainright, Alberta, and released in Wood Buffalo Park between 1925 and 1928. At present the bison are most abundant on the meadows of the Peace River delta, north of Lake Claire. The total number in the park in 1961 was about 10,300 according to an aerial census made by Novakowski (letter to Fuller, 1961).

The bison herd in Waterton Park was started in 1952 with the introduction of five cows and a bull from Elk Island Park. These animals bred successfully, and in 1955 and 1958, slaughters were held to reduce the herd to a size that the range could support. New bulls were introduced in July 1955 and May 1958, the policy being to reduce inbreeding in the herd. By the spring of 1961, when my study began, the herd numbered 25 animals.

The Habitat of the Waterton Bison

The enclosure in which the Waterton herd is kept is under three-quarters of a section in area, and is divided into a winter pasture of a little less than a quarter-section, and a summer pasture a half-section in size. When my study

began the bison were in the winter pasture, where they had been since the fall of 1960. On 6 June 1961, they were herded into the summer pasture, where they remained during the rest of my study. The enclosure is in open rolling grassland in the foothills of the Rocky Mountains. There are few trees in the area. The largest stand is about one acre of aspen poplar, *Populus tremuloides*, in the winter pasture, and the total area covered by trees is less than three acres.

The Composition of the Waterton Herd

The composition of the Waterton herd, and the ages of some of its members, are shown in Table I. The numbers used to identify the animals are explained later. They are the same as those in Fig. 6, and used throughout most of this paper. All bulls have a number preceeded by the letter B; all cows have the letter C.

The herd numbered 25 animals at the beginning of May. It included a three-year-old bull, B.10, that had partly paralysed hind legs. In June, 1961, this animal was attacked by the rest of the herd, was badly injured and had to be destroyed. Seven calves were born in the herd while I was there. Their birth dates are given in Table III. With the addition of these calves, and the death of the young bull, the herd numbered 31 animals when I left on 15 August 1961.

Table I. Composition of the Waterton herd, early May 1961

Animal number	Age (in years)	Age and Sex Class			
		Adult bull	Adult cow	Sub-adult bull	Two-year-old or yearling
B.1	5 or 6	x			
B.2	7 or 8	x			
B.3	5 or 6	x			
B.4	5	x			
B.5	4			x	
C.1			x		
C.2			x		
C.3	4		x		
C.4			x		
C.5			x		
C.6			x		
B.6	2				x
C.7			x		
C.8			x		
C.9			x		
B.7	2				x
B.8	2				x
B.9	2				x
C.10	3 or 4		x		
C.11	3 or 4		x		
C.12	3 or 4		x		
C.13	2				x
B.10	3			x	
B.11	1				x
C.14	1				x

In interpreting the social relationships of members of an animal society it is useful to know the ages of the individuals. Unfortunately only a few members of the Waterton herd were of known age. Records of the number of calves born each year had been kept since the herd was started. This served as a check in the identification by their appearance, of yearlings, two-year-olds and three-year-olds. The animals slaughtered in 1958 were not aged accurately, so I could not tell how many bison belonged in each age-group older than the three-year-old group. Where ages of animals were known or were almost certain, they are entered in Table I.

According to the records there were two yearlings, five two-year-olds and four three-year-olds. Two-year-olds are easy to distinguish by their appearance, and so their ages are not queried. There was one three-year-old bull, B.10, the cripple. This animal's age was checked after its death, by the development of its teeth (see Fuller, 1959). Three- and four-year-old cows are not easy to distinguish. However, the three youngest looking cows after C.13 were C.10, C.11, and C.12, and I think these were the three-year-olds. The only other animal whose age was certain was a four-year-old cow, C.3, recognisable by having one broken horn, an accident that occurred in 1957 when she was a calf. B.5 was almost certainly four years old, judging by comparison of his

appearance with that of several four-year-old bulls* in Elk Island Park. By calculation from the herd records, and from their appearance, B.4 and B.1 were five years old, B.3 was six and B.2 seven years or more.

General Activity of the Herd

The Waterton herd behaved in general as a unit, with all herd members taking part in such activities as grazing and drinking, at the same time. An exception was the crippled three-year-old bull. This animal often lagged behind the herd during grazing activity, following about 30 yards behind. It sometimes behaved independently -- grazing, for example, when the rest of the herd was lying. There was also a tendency for the five largest bulls, B.1 to B.5, and the cows C.1 and C.2 to graze and lie down close together, forming a sub-group. This was particularly noticeable during May and June, but during July this sub-group broke up. During July and August B.1 and B.2 were often to be seen alone, but the other members of the sub-group rejoined the main herd. When C.1 calved on 23 May, she left the bull sub-group and returned to the main herd, but about a month later, she was to be seen more and more often with the bulls. Her calf would remain with the other calves, and she would return to it to feed it.

The chief activities of the herd were grazing,

---

* These bulls were branded as calves in 1957.

ruminating and resting. It soon became apparent that there was a rhythm to these activities, with grazing periods alternating with those of resting, and with ruminating occurring at the beginning of each resting period. There were usually three grazing periods between 7:00 a.m. and 10:00 p.m. Corbett (1953) found a similar rhythm of activity in domestic cattle (Bos taurus domesticus). In the Waterton bison, the three grazing periods occurred between 9:00 a.m. and 11:00 a.m., 2:00 p.m. and 5:00 p.m., and between 7:00 p.m. and 9:00 p.m. Various activities other than grazing also occurred during these times, Drinking was most frequent during the afternoon or evening grazing period. Wardrop (1958) found that domestic cattle usually drank after 3:00 p.m. Rutting behavior was most intense at the beginning of each grazing period, and suckling also usually occurred at that time. General activity was highest during the evening grazing period. Much wallowing and rubbing of trees also took place at that time. Figs. 1, 2, and 3 show the Waterton herd during the evening activity period, during a resting period, and drinking at a lake.

Unlike the activities mentioned above, salt licking usually took place during a resting period. This was usually immediately before the morning grazing time. During salt licking activity, most of the herd members would be lying down, with the only animals standing being those using the salt or trying to do so. Many interactions occurred as one

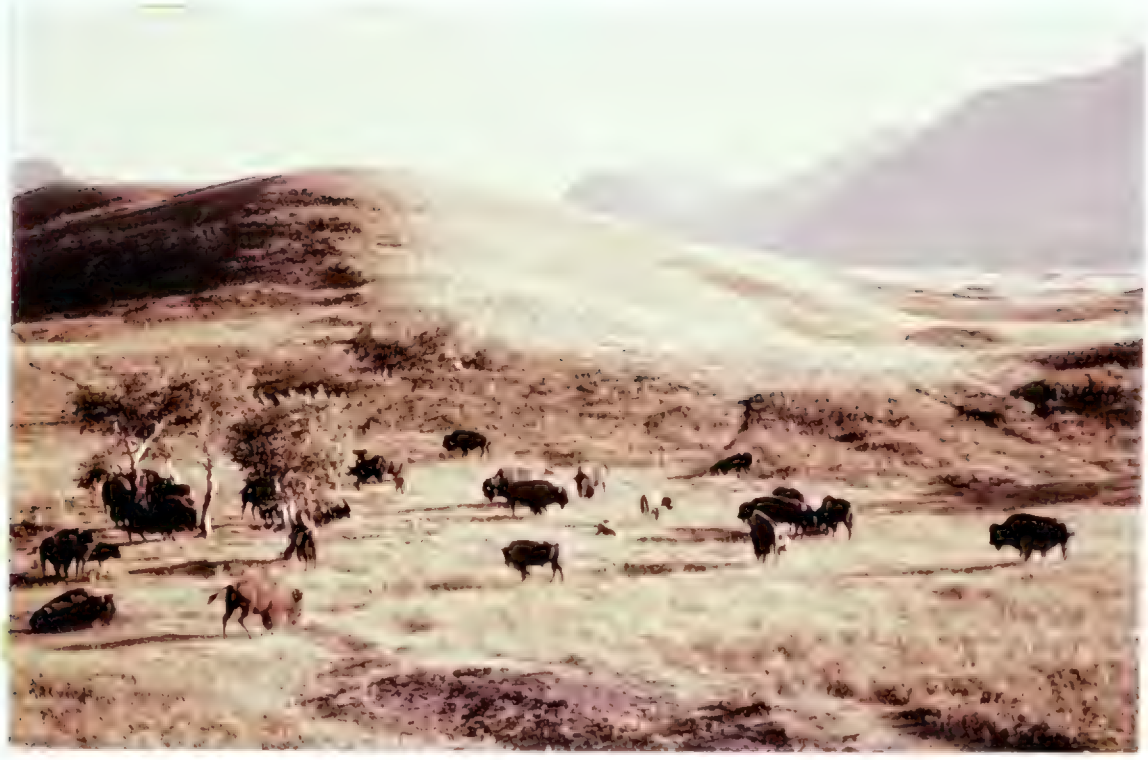


Fig. 1. The Waterton herd during the evening activity period. Note different animals grazing, wallowing, rubbing on trees, and suckling.

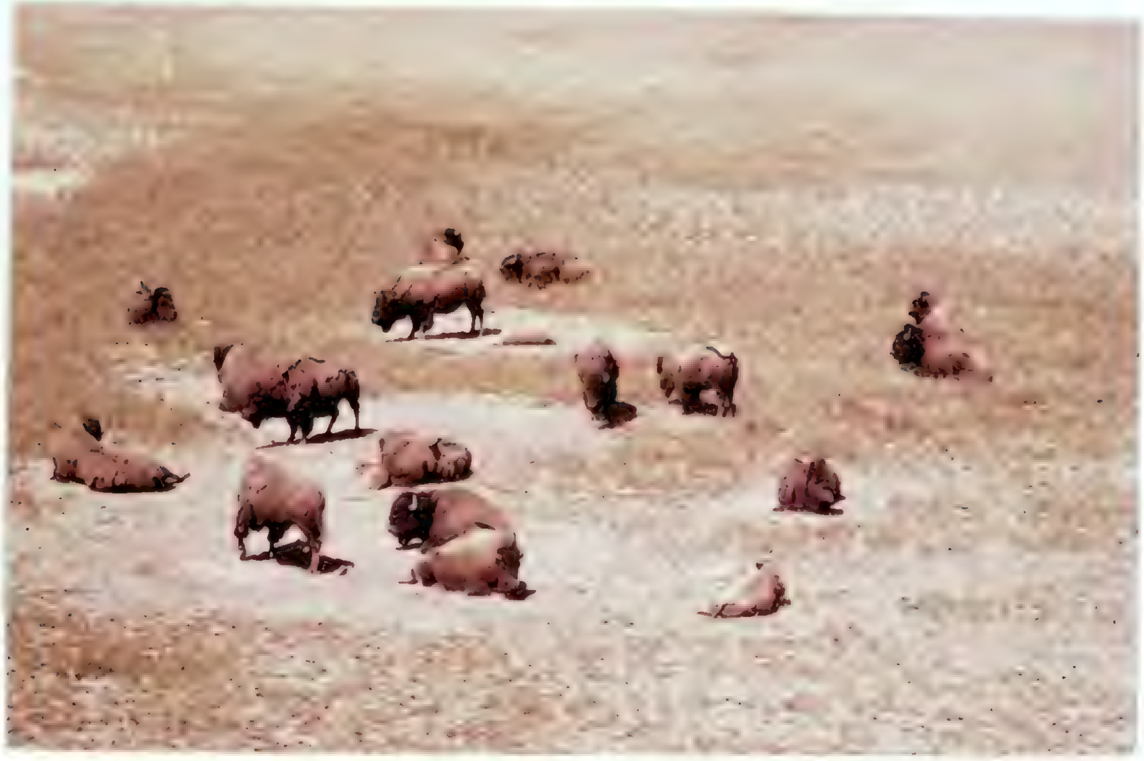


Fig. 2. The Waterton herd during a resting period.

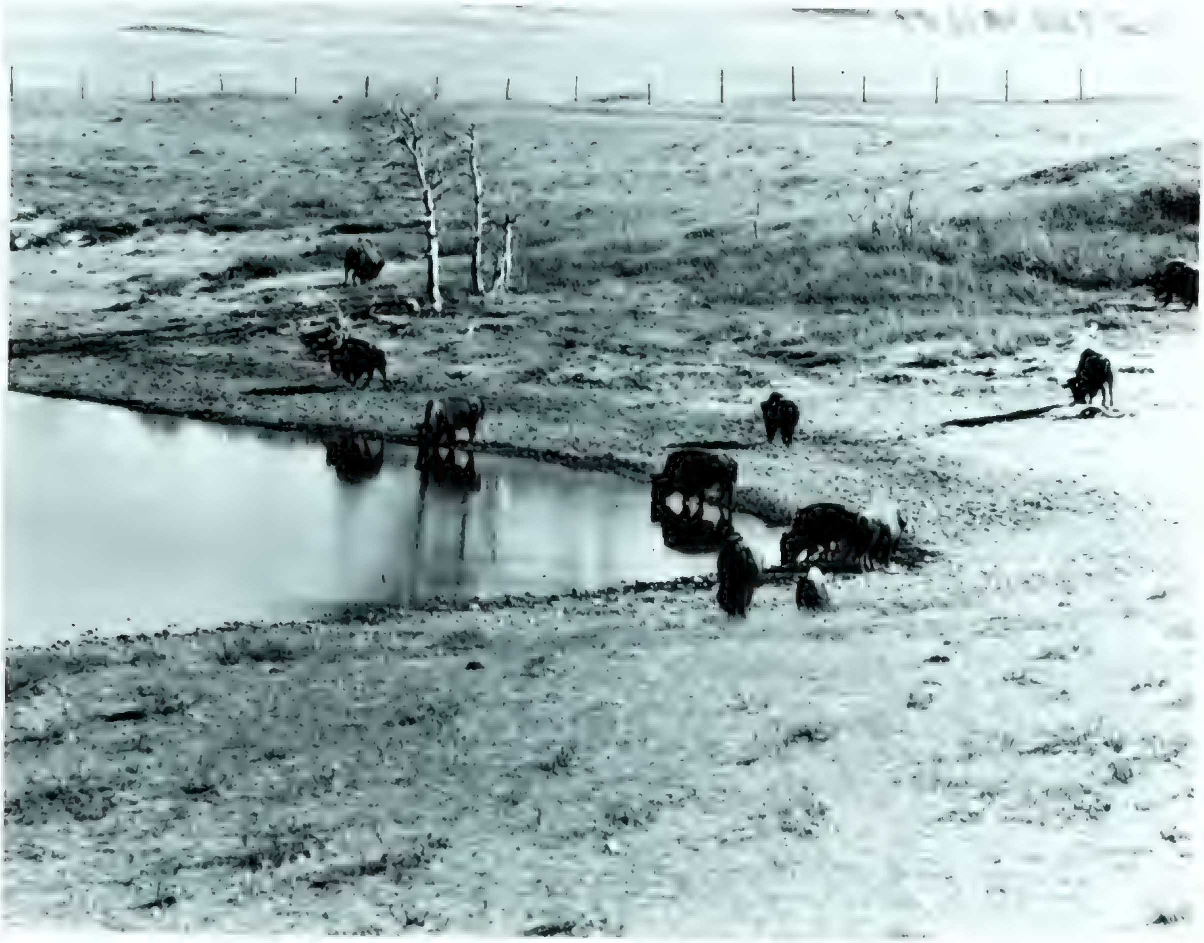


Fig. 3. The Waterton herd drinking at a lake.

animal replaced another at the lick. Sometimes, one animal would stand and wait while another licked.

The herd usually spent the hottest part of the day, between 11:30 a.m. and 2:00 p.m. resting. Periods of lying down began gradually. The grazing herd would slow down, then stop moving, and then graze in one place instead of walking along. Then one animal after another would lie down and begin to ruminate. It usually took more than half an hour before the whole herd was lying. The last animals to stop feeding were usually adult bulls and pregnant or lactating cows. During the second half of the resting period, most of the animals would stop ruminating. Some animals, particularly calves, but also yearlings and two-year-olds, often lay flat on their sides, apparently asleep. Older bison seldom lay flat, and if they did, it was only for a few minutes at a time. Probably the rounded shape of the ribs of adult bison makes lying flat uncomfortable.

The herd showed a tendency to be in a certain part of the pasture at a given time of day. Thus, during the time the herd was in the summer pasture, on 34 out of 58 mornings when I looked for the herd between 7:00 a.m. and 9:00 a.m., it was in the same area near one of the salt licks. During the evening period of activity the herd was usually near one of the lakes where the animals drank, or near the largest group of trees, where there were several wallows, and most rubbing on trees occurred.

Effects of Weather on Behavior

There was evidence that weather conditions affected the general activity of the herd. During very hot weather grazing was reduced, and the herd would lie in the open, usually near a mud hole. On one occasion, when the wind was over 70 m.p.h., the herd lay on the sheltered side of a hill all day, and did not graze at all until the wind died down in the evening. The herd was once seen to stampede during a severe hail storm, the animals running with their backs to the wind. Prolonged heavy rain stopped grazing activity, and the bison stood with heads low and backs humped. Light rain did not alter grazing behavior, but play, fighting and rutting were much reduced in frequency during rain.

Description of Certain Behavior Patterns

McHugh (1958) has described most of the behavior patterns occurring in bison. There are a few, however, that I observed and that he did not mention. I shall describe these briefly here.

The "Gape"

This is a behavior pattern closely resembling a yawn. It differs from the ordinary yawn in that the animal does not breathe while showing this behavior. The posture is also held for a shorter time than during yawning. This behavior occurred only rarely. It was shown after a bison

had just sniffed a newborn calf. It was most often seen in the calf's mother, but other bison sniffing the calf soon after its birth, also showed the behavior. I do not know what significance, if any, this behavior has.

"Heading-off"

This is a behavior pattern occurring in calves, that is used to stop a calf's mother from walking along, so that the calf can suckle. It is described in detail in the section on calf behavior, so I shall not discuss it further here.

"Head-wagging"

This behavior consists of a vertical swinging motion of the head of the animal. Unlike the jerking motion of threat behavior, it is a smooth, swinging motion. It usually occurred in bulls that were involved in play-fighting. It occurred during a pause in the fight and was usually shown by the higher ranking member of the pair. The fight would begin again with renewed vigor after this behavior, and I think it functioned as an invitation to continue the fight. I occasionally saw this behavior performed by an animal waiting by a salt lick for a more dominant animal to stop licking. Here, perhaps it functioned as an invitation to begin a fight* over the salt.

---

* The type of fighting that occurs in competitive situations is discussed in the next section (p. 21).

The "Lip-curl" Posture

The "lip-curl" is a behavior pattern usually associated with rutting behavior. It has been mentioned, but not fully described, by McHugh (1958). When showing this behavior, the animal extends its neck forward, raises its head, and curls its upper lip upward (Fig. 16). Sometimes the head is moved sideways at the same time. This behavior was shown far more often by bulls than by cows. The posture was usually held for 10 or 11 seconds, but was occasionally held for as long as 15 to 17 seconds in adult bulls. The lip-curl behavior was always preceded by the animal sniffing something -- either an object on the ground or another animal. I consider it as a separate behavior pattern from sniffing, however, because sniffing often occurred without the lip-curl following. The significance of this behavior, and the circumstances of its occurrence are discussed in the section on rutting behavior.

THE DOMINANCE HIERARCHY

Introduction

As Woodbury (1941) pointed out, it has been known to farmers for many years that a "hook order" or dominance hierarchy exists in herds of domestic cattle. Seldom, however, have such social groups been studied in detail, or the findings published. Schein and Fohrman (1955) analysed the social hierarchy of a large herd of dairy cattle, and Schloeth (1961) found that there was a dominance order in the herd of semi-wild Camargue cattle (*Bos taurus camarguensis*) that he studied. McHugh (1958) found a dominance hierarchy existed in a herd of 16 bison in the Jackson Hole Wildlife Park in Wyoming.

In the herd studied by McHugh, 90 per cent of the interactions upon which the hierarchy was based were recorded when the herd was eating hay and concentrates fed to them during the winter. Communal feeding of bison in a restricted area represents an unnatural situation, and the hunger of the animal at the time of an interaction, could influence its aggressiveness with another animal. My main purpose in deciding to investigate the dominance structure of the Waterton herd was to see if more naturally occurring interactions would give evidence of the existence of a dominance hierarchy.

Methods

In order to obtain accurate information on the social relations between herd members, it was necessary to be able to recognize them individually. For that reason I initially planned to mark the animals with paint. However, when I arrived in Waterton in May 1961, the bison had begun to shed their winter coats. This meant that unless they could be marked on the horns or hoofs, the marks would soon be shed with the winter hair. It soon became clear, however, that there would be little difficulty in distinguishing the animals by their sex and size, and by individual characteristics such as shape of the horns, and so I gave up the idea of marking them with paint. Within one week, 10 of the bison could be distinguished, and by the end of five weeks, I could recognize each animal individually.

For convenience in taking notes, I named each animal according to the characteristic by which I recognized it, and then shortened this name to initials. Thus, for example, an animal with a crooked horn was written as C.H., and a cow with a broken horn became B.H. The five largest bulls were easily distinguishable by size, and were numbered B.1 to B.5, accordingly. I named the seven calves a to g, in order by their age, as they arrived. Calves could be distinguished by their size, and by changes in coat color as they grew older.

Only interactions between individuals that I was sure I recognized were included in the analysis of the social

structure of the herd. Thus, a few of the interactions recorded during my first month at Waterton, were not used.

Threat Behavior

The interactions recorded in this investigation were those termed 'aggressive'. Whether or not an action was one of aggression was determined partly by the nature of the action itself, and partly by the reaction of the animal towards which the action was directed. The actions classed as aggressive formed a series of increasing severity, as follows: (the aggressor is A, and the animal towards which the aggression is directed, is B)

1. A walks towards B
2. A turns head towards B
3. A jerks head up and down, towards B
4. A thrusts head sideways at B, so that one horn is nearest to B
5. A makes a running lunge and a head thrust at B

In number 1. above, the walk differed from the way an animal walked normally. There was a "purposeful" look about it, the movements were a little jerky, and the head was sometimes jerked slightly up and down at the same time. Aggression of the type in 4. above, is illustrated in Fig. 4. The aggressor is the bison on the right.

The reaction of animal B depended upon the severity of the aggression shown by A. It ranged from turning slowly away from A and returning, to leaping out of the way of the

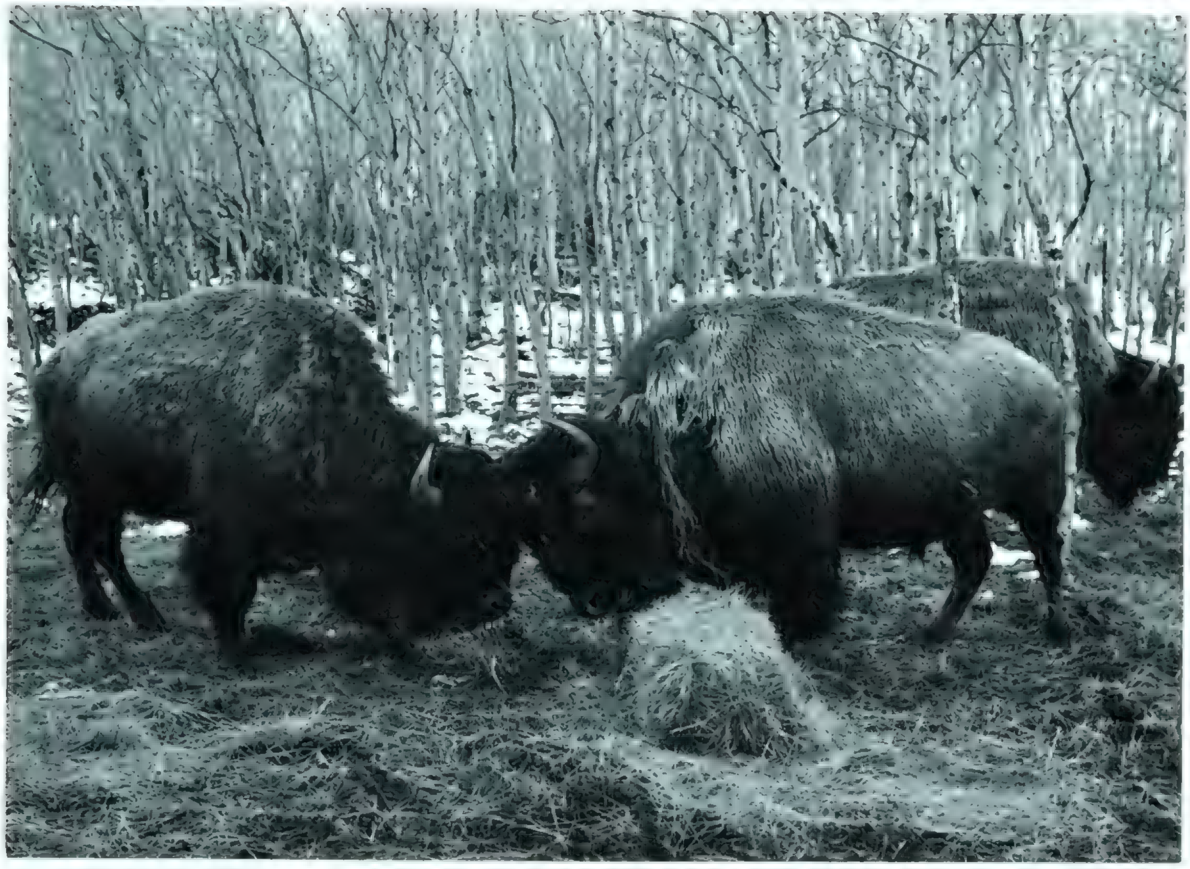


Fig. 4. Threat behavior over a hay bale. The bull on the right, B.1, was dominant to the other, B.4.

lunging type of attack (number 5), and staying away. Sometimes, when B returned after a mild aggressive act from A, A would then show increasingly strong aggression until B stayed away. This sort of interaction often occurred when a yearling tried to investigate a calf and the calf's mother drove the yearling away.

Another type of aggression was a mild form of fighting or "wrestling" that usually occurred over hay or a salt lick. The two combatants would lock horns and push one another with their foreheads. This type of fighting, illustrated in Fig. 5, lacked the viciousness of the fighting that occurs between rutting bulls, and resembled play-fighting (discussed later).

During the first ten days of May 1961, the Waterton herd was fed a small amount of hay, and 7 per cent of the 1155 interactions recorded in Fig. 6 were aggressive interactions occurring over the hay. Other aggressive interactions recorded were the result of competition for rubbing trees, wallowing places, objects of curiosity and salt licks. Cows showed aggression towards other bison investigating their calves, and bulls displaced one another while investigating cows. Interactions of these types were recorded.

"Passive Displacement"

Another type of interaction recorded was "passive displacement" of one animal by another. It soon became noticeable that as the herd walked along, some members would

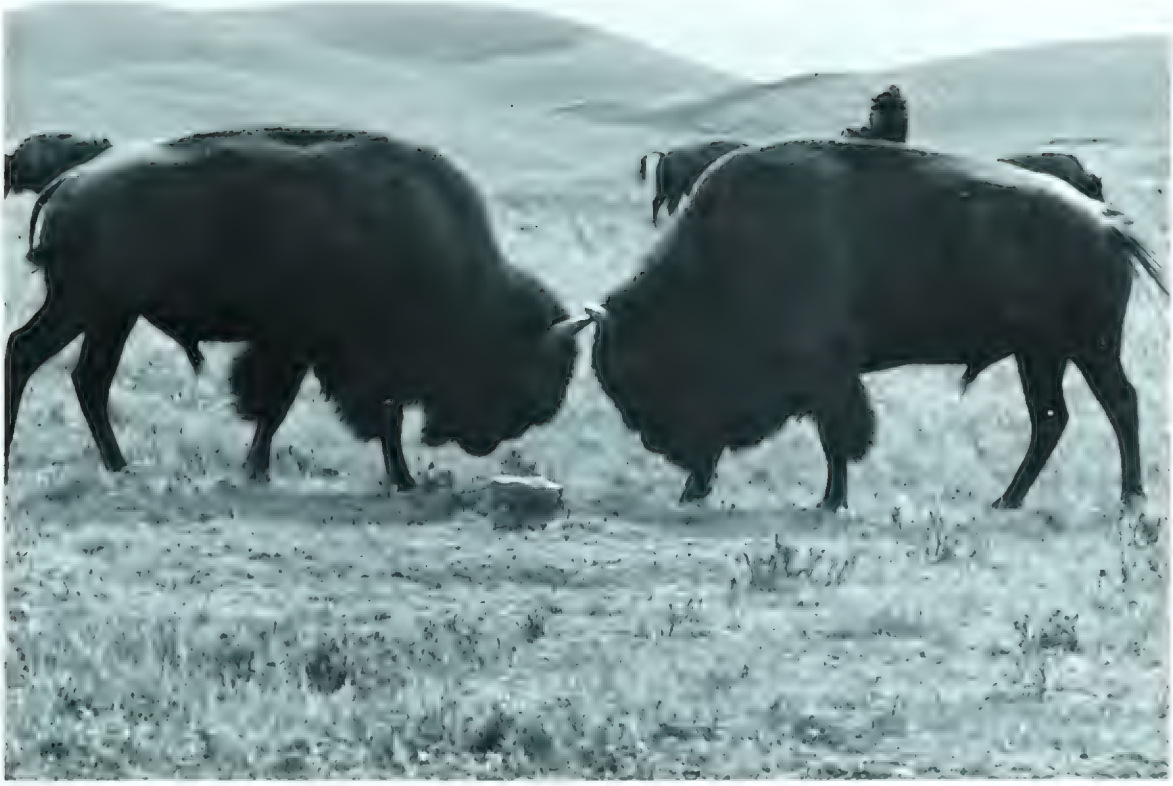


Fig. 5. "Wrestling" over a salt lick. The combatants are B.4 (right) and B.5 (left).

walk faster when certain others were behind them, or one animal would move out of another's way, without any noticeable aggressive action taking place. The same sort of thing happened as the herd stood up before moving off to graze. If one animal stood up and walked forward, certain others in its path would get up and either walk ahead of it or move sideways out of the way. It was particularly noticeable that such a move by one of the adult bulls was followed by a chain reaction of bison getting up and out of one another's way, and that these reactions were consistent: certain herd members always moved away from certain others. I decided to see if such interactions could be used as an index of dominance, so I plotted them separately from other types of reactions, and compared the two sets of results. The results showed that an animal that moved away from another at a salt lick or a wallow would also get up and out of that animal's way as the herd was beginning to move. Animals that were dominant in situations in which there was competition for something, could start off a chain reaction of herd members standing up, while subordinate ones did not. Such passive displacement reactions formed about 40 per cent of the interactions used in assessing the dominance hierarchy.

Results

The result of the analysis of the social interactions between known individuals is shown in Fig. 6. Each figure represents a certain number of interactions between two

LOSERS

WINNERS

animal number	B.1	B.2	B.3	B.4	B5	C.1	C.2	C.3	C.4	C.5	C.6	B6	C.7	C.8	C.9	B7	B8	B9	C.10	C.11	C.12	C.13	B.11	B.12	C.14	a	b	d	c	e	f	g	total wins
B.1		24	9	17	5	7	6	4	5	1	2	1	2		2			1		1			1			2							90
B.2			9	12	7	12	8	8	1		5	3	4	3		1		1	3	3	3	1	1			1	3		2			1	92
B.3				7	5		4	6	3	4	1		1	2	2	2	3			1	2	4			2				1				50
B4			5		10	8	6		1	1	2	2		1		3	3	4		1	3				1	3	1	1	3				59
B.5	1		2			3	4	2	2		2	7	2	6	1	3	4	4	2	3	4	1		2		2							57
C.1							9	7	6	4	4	5	4	2	1	1	4	1	1	7	4	8	1	1	10	9	4	1	2			2	98
C2								8	1	9	5		4	1	4	3	1	6	2	2	6	3			3	2	10	1	1			8	80
C3							1		7	7	3			3	4		4	1		1	2	4		2	1	1		1	2				44
C4							2			2	7	3	10	5	3	1	3	1	2	4	5	5		8		7	5	1	5				79
C5									1			4	3	3	5	3	1	3		1		3			2	2		2		1		1	35
C.6										3			3		5		4	1	2		3	3			1		1		1	1		1	29
B6								2	1	1			1		2	2	8	5		2		1			1	1	1		1		1		30
C.7														5	1	1	3	5	1	5	6	5		4	11	6		2	2	3		3	63
C8			1												5			1			5	2		1	1	1	1		1				19
C.9									1				4	1		3	4	2	3	1	1	2		9	1	2				1			35
B7									2				1	2			4	5	1			1		4	1	1		2	1				25
B8				1									2	5		1		4	2	7	6			1		8	2	1	2		5		47
B9													1		1	1	2			2	1			1	5	2	3		2				21
C.10																				2	9	1	1	2	1	1	1	3	3			3	27
C.11																1	1				6	5		5	4	3	6	2	2				35
C.12				1							1				1	2			4	1		2	1	3	2	8	2	2	10	3		1	44
C.13																							2	6	4	3	2		3				20
B.10																																	0
B.11																	1								10	2			3				16
C.14																										5	4		4				13
a																											7	6	4				17
b																													3	2	2		7
d																													6	3		3	12
c																											2	2		2	1		7
e																																1	1
f																													1			1	2
g																														1			1
total losses	1	24	26	38	27	30	40	37	31	32	32	25	42	39	37	28	50	45	23	44	66	51	7	49	61	72	55	27	65	17	9	25	1155

Fig. 6. Dominance hierarchy in the Waterton Park herd, summer 1961.

individuals. In a chart of this type, if wins and losses between individuals occurred at random, about 50 per cent of them would appear on each side of the diagonal line. If the hierarchy were perfectly linear, with a transitive relationship between all the animals, (i.e. if it were always true that if A was dominant to B, and B was dominant to C, then A was dominant to C), and if there was no aggression by subordinate animals against higher ranking ones, then all the entries would be above the diagonal. An entry below the diagonal means that an animal has won an interaction against another to which it appeared, as a result of other interactions, to be subordinate, or it may show the presence of a triangular relationship between three animals. As the chart shows, an almost linear hierarchy existed in the Waterton herd, with fewer than 6 per cent of the entries being below the diagonal.

When it became clear that his dominance hierarchy existed, each herd member was given a number according to its rank. (These are the numbers used in Table I.) The bulls were numbered B.1 to B.11. This meant a rearrangement of numbering in the five largest bulls, because their rank order was not the same as their order in size. The cows were numbered C.1 to C.14. These rank numbers rather than the original names will be used throughout this paper in referring to animals other than calves. The calves were not renamed, because with only one exception, their rank order was the same as that of their age, and, as mentioned earlier, the calves were originally named according to their age.

The number of times that an animal dominated any other can be found by reading along the rows in Fig. 6, while the columns indicate the number of times an animal was dominated. Thus, for example, B.1 dominated C.1 seven times, and C.2 was dominated by B.2 eight times. The total wins of each animal are shown in the row totals; the total losses in the column totals. An animal was said to be dominant to another if it won more contests than it lost, against that animal.

The severity of an aggressive action varied according to the individuals involved. In general the most severe aggressions and the wrestling interactions were between animals close together in rank. Wrestling was particularly common between B.3 and B.4 and between B.7, B.8, and B.9. Aggression between animals that were far removed in rank was usually only mild. An animal high in the hierarchy would displace a low-ranking one just by walking towards it, or by a gentle jerk of the head. A striking example of this was that a bull had only to look at a calf, and the calf would run away. This variation in severity of aggression and the passive displacement interactions that were discussed earlier, led me to believe that the bison in the Waterton herd could recognize one another individually.

Discussion

As Fig. 6 shows, the dominance order in the Waterton herd was ~~a simple~~ an almost linear one. There are certain features of it, however that should be pointed out. One of these is that not every member of the herd was involved in an aggres-

sive interaction with every other member. This is why there are some gaps in the chart. In such cases, I had to assume a certain relative rank order for the two individuals, from that of the animals nearest to them in rank. Thus for example, there was no interaction between B.4 and C.3. Because B.4 was dominant to C.1 and C.2; and C.1 and C.2 were dominant to C.3, I assumed that B.4 was also dominant to C.3. The crippled bull, B.10, interacted so seldom with other members of the herd that it was impossible to place him in the hierarchy using the same criteria as for the rest of the animals. I placed this bull immediately below the lowest ranking animal that was seen to dominate him. This was the cow C.13. B.10 never interacted with either of the yearlings, B.11 and C.14, or any of the calves, but I assumed that it would have dominated them had they interacted.

There are three places in the hierarchy where the relative rank order of certain animals is questionable. The first of these is the case of B.3 and B.4. B.3 won seven interactions over B.4, but lost to B.4 five times. Another case is that of three bulls, B.7, B.8 and B.9. Although there appears to be some order among these three animals, the difference between the number of wins and the number of losses of one animal in respect to the others is small. The third case is one where there appears to be a triangle in the rank order of the three cows, C.7, C.8 and C.9. Here, C.7 was dominant to C.8 and C.8 to C.9, but C.9 appeared to

be dominant to C.7. Possibly, if I had observed a larger number of interactions between these three animals, the situation would have become clearer.

The ages of some members of the herd have been discussed previously. Certain conclusions can be drawn about dominance in these known-aged animals. Yearling and two-year-old bulls were dominant to cows of the same age-group. Two-year-old bulls were also dominant to three-year-old cows. B.6, a two-year-old larger than B.7, B.8 and B.9, was not only dominant to the three-year-old cows, but also to three other cows that were four or five years old.

Schein and Fohrman (1955), in their study on domestic cattle, found that there was a strong positive correlation between the dominance status of an animal and its age and weight. I did not have the weights of any of the Waterton herd members, and, as already mentioned, few of the older animals were of known age. It appeared that in some cases age was an important factor in determining rank, but not in others. I think that the cows were ranked partly by age and partly by size. For example, the highest ranking cow, C.1, was a small animal, but looked older than the others. C.3, on the other hand, was only four years old, but was a large animal, and this perhaps explains her rank. However, as Schein and Fohrman (1955) pointed out, there are probably other factors, including agility of the animal and

individual differences in temperament, that could be important in determining rank. An unexpected situation existed among the five highest ranking bulls. The oldest, largest and heaviest bull was second in rank to a smaller bull, two or more years younger. One might expect this in the case of an aged animal, but B.2 was probably not more than seven or eight. B.1 was also smaller and probably a year younger than B.3. Thus, age and size were not the critical factors in determining the rank of these bulls. In the three two-year-olds, B.7, B.8 and B.9, also, size was not the determining factor in their relative positions in the hierarchy, since B.7 was the smallest of the three.

The most interesting aspect of the analysis of the social hierarchy of this group is that it revealed the tendency of some herd members to react more often with certain animals than with others.

In the chart, Fig. 6, most of the high entries occur close to the diagonal line, showing that an animal reacts more often with those close to it in the hierarchy than with those further removed. This is illustrated in Fig. 7 which shows the total observed interactions and total theoretical interactions (see below) between animals different distances apart in the dominance hierarchy. I shall refer to the relative distance of any two animals as their "proximity number". Thus for example, two animals ranked one position apart have a proximity number of one. In Fig. 7

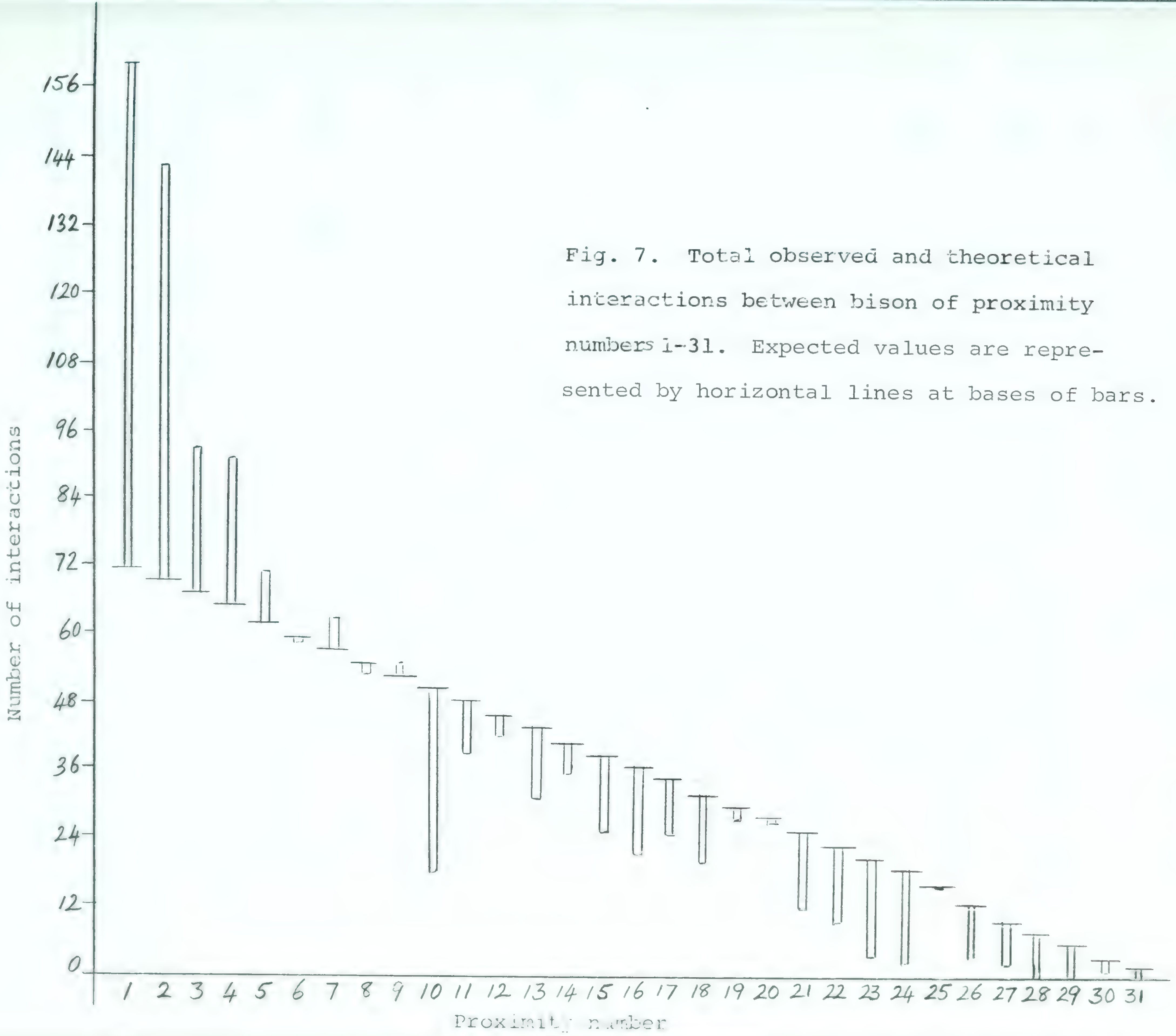


Fig. 7. Total observed and theoretical interactions between bison of proximity numbers 1-31. Expected values are represented by horizontal lines at bases of bars.

the horizontal lines show the theoretical totals, and the vertical bars show the difference between the theoretical and observed totals.

Fig. 8 is an explanatory diagram showing how the theoretical and observed totals were calculated from the values in Fig. 6. The observed totals were calculated by adding the figures along the appropriate diagonals. For example, the "proximity one" total is the sum of the entries along the two diagonals labelled proximity one. The theoretical totals were obtained from the values that would occur in each square of Fig. 6 if interactions occurred at random. The theoretical value per square was obtained by dividing the total observed interactions (1155) by the number of squares (992): $\frac{1155}{992} = 1.16$. Hence the theoretical total for each proximity number is 1.16 x the number of squares on the diagonals in question. For example, the theoretical total for proximity one is 1.16 x 62 = 71.9. Since there are 31 pairs of animals with proximity 1, and only one pair with proximity 31, the theoretical totals drop as the proximity rating drops from 1 to 31.

From Fig. 7, it can be seen that for animals up to four positions apart, the number of interactions is considerably higher than the theoretical values. After four positions, it appears that the number of observed interactions approximately fits the theoretical, but the values are offset, because a high proportion of the total 1155 interactions

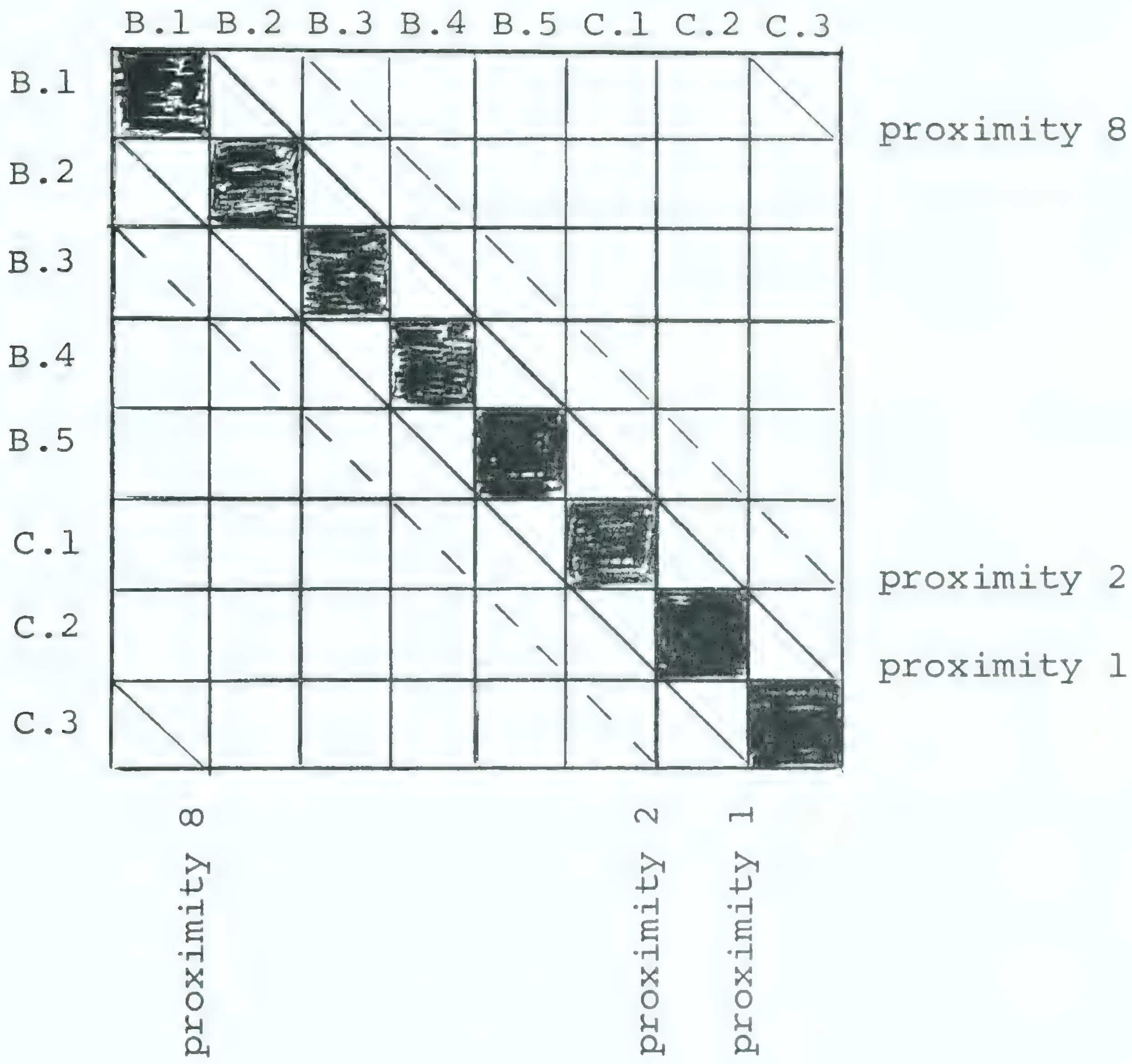


Fig. 8. Diagram of a portion of the chart, Fig. 6, to show how total observed and theoretical values were calculated.

[illegible]

occurred in the first four positions, and the theoretical values are high, having been calculated from the total 1155. In order to compare in a more meaningful way the observed and theoretical totals for animals 5 to 31 positions apart, new theoretical totals were calculated, disregarding the values for the first four positions. In order to eliminate bias, new values were calculated four times, first omitting the values for proximity 1 to 4, then 1 to 5, then 1 to 6, then 1 to 7.

The new theoretical totals calculated, omitting the values in the first seven positions, are shown in Fig. 9. The total observed interactions, omitting the values for proximity 1 to 7, was 474, and the total number of squares was 600. Thus the new theoretical value per square was .79. It can be seen that the observed totals (which are the same as in Fig. 7) closely fit the theoretical ones.

Results similar to those in Fig. 9 were obtained when calculations were based on the omission of the values for the first 4, first 5, and first 6 proximity numbers, but the best fit of the observed to the theoretical totals occurred when the first 7 sets of values were omitted.

It can be concluded, then, that in the Waterton bison herd, interactions were much more frequent between animals of proximity 1 and 2 than would be expected on the basis of chance. This was also true, but to a lesser extent, for animals of proximity 3 and 4. For proximity ratings

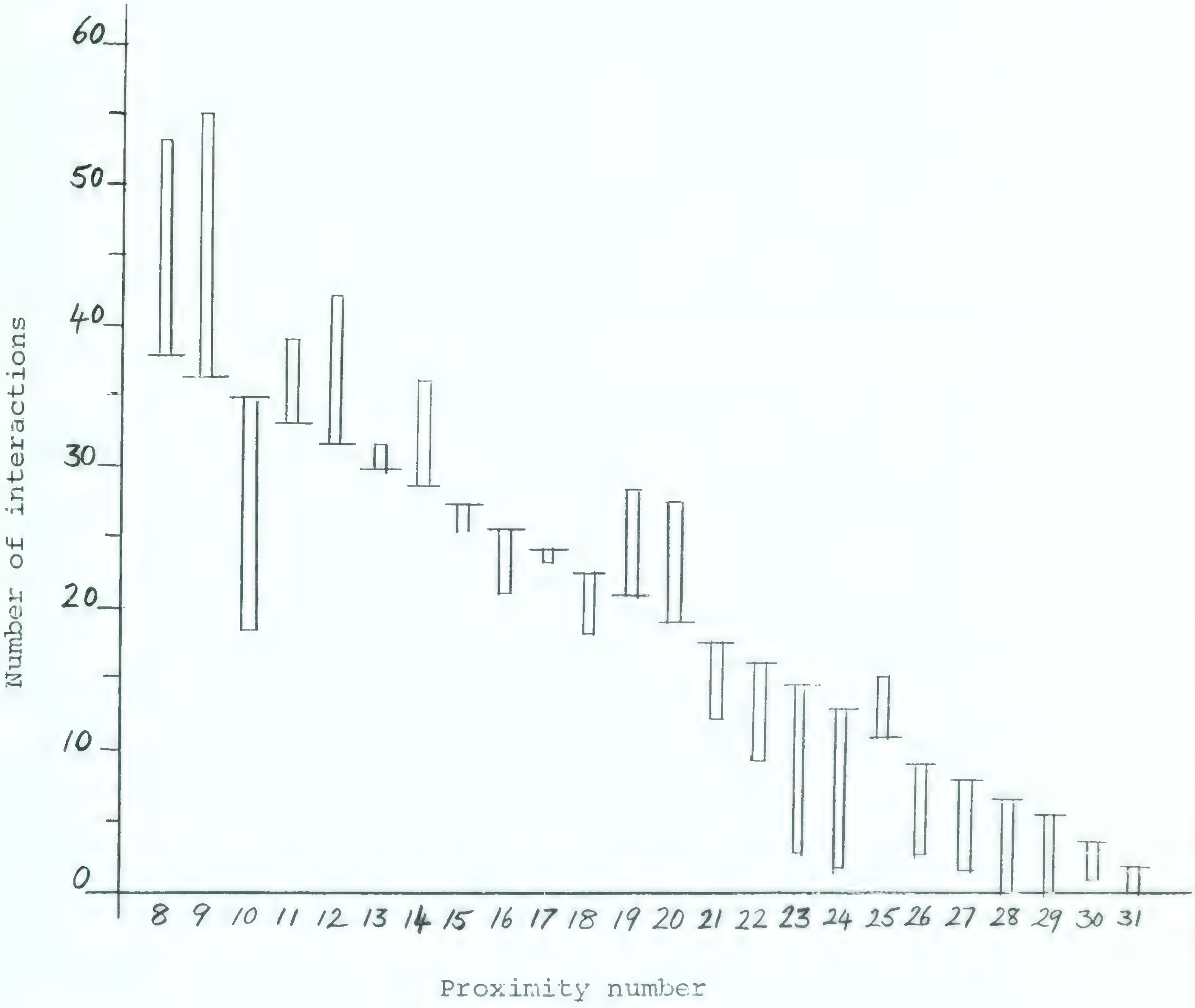


Fig. 9. Total observed and theoretical interactions between bison of proximity number 8-31.

between 5 and 22, however, the frequency of interaction was about what would be expected, if interactions occurred at random. Thus, whether two animals were 5 or 22 places apart in the hierarchy, interactions between them occurred with about the same frequency. For proximity ratings between 23 and 31, however, interactions were mostly fewer than expected.

The cows with calves, C.1, C.2, C.4, C.7, C.10, C.11, and C.12 tended to interact frequently with the yearlings, B.11 and C.14, and with the older calves, a and b. This was because the yearlings and older calves showed more interest in young calves than the other herd members did, and cows were aggressive towards them, preventing investigation of their calves.

The chart also shows up the fact that some herd members were more active than others. The total number of interactions recorded for any one animal varies between 7 for B.10, and 133 for C.1, the highest ranking cow. In general it appears that the most active members of the herd, as judged by the number of interactions in which they were involved, were the five highest ranking bulls and the cows that had calves. These are in part explained by the frequent interactions between bulls in competitive situations such as feeding at hay, and the numerous interactions between cows and the animals that tried to investigate their calves.

When I began the investigation of the social structure of the Waterton herd, all I was expecting to find out was whether or not there existed a dominance hierarchy. It

can be seen that other unexpected information emerged about the relationships between different members of the herd. This shows that although previous studies may already have revealed the existence of dominance hierarchies in societies of a given species, it is not a waste of time to repeat such studies, because unexpected information may well come to light. I think the method used in Fig. 6 to plot the interactions is particularly helpful in revealing the relationships of one member of a herd with another.

The Significance of Dominance

Probably the most important result of the existence of a dominance hierarchy in an animal society is that it prevents fighting that could result in the injury of the animals. This was, I think, the prime significance of the hierarchy in the Waterton bison. Especially in a competitive situation, for example when two bulls go for the same wallow or rubbing tree, it is an advantage to the animals that one gives way to the other, and they do not injure one another fighting.

The significance of dominance in connection with cows and their calves, is discussed in the section on calf behavior.

A third result of dominance follows from the passive displacement of one animal by another, which I discussed earlier. The fact that only the dominant animals could cause

several members of the herd to stand up and start moving, meant that only the adult bulls or high ranking cows could start a herd movement, as for example, when the herd began to feed after a resting period. Thus, dominance plays a part in leadership in such a situation.

THE BEHAVIOR OF CALVES AND THE RELATIONSHIP BETWEEN COW AND CALF

Introduction

The cow-calf relationship and the development of the behavior of the calf was the main subject of my work. There has been no published study on this subject, and apart from a few references in the historical literature, the only information on the behavior of bison calves is in a short section of McHugh's work (1958).

My work on this aspect was done at Waterton. During the time I was there, seven calves were born in the herd. My data are based on observation of the birth of two calves and on the later behavior of the seven calves. This may seem a small number from which to generalize, but the behavior of the seven calves was consistent, and I could find no differences between the behavior of the calves at Waterton and those in the wild bison in Wood Buffalo Park, so I do not think there is anything to suggest that these seven calves were not representative of bison calves in general.

The Calving Season

The calving season in bison is from April to June (McHugh 1958, Soper 1941), with some variation between areas. Comparison of information for Wood Buffalo Park (Soper 1941 and K. F. Cooper, pers. comm.) with McHugh's data for the bison herds in the United States, suggests that the calving season is about two weeks later in the northern herds than

in the south. In the Waterton herd, there is a less distinct calving season. Herd records show that over the years since 1952, when the herd was started, calving has generally been from April to July. In 1961, 11 calves were born,--two in May, two in June, three in July, two in August, one in September and one in December. In 1962 there were no calves in this herd until June, when four calves were born. A fifth calf was born in July, and another two in August, 1962.

Physical Appearance of the Pregnant Cow

In some cases, the rounded appearance of the body, and a sharp hollow between the abdomen and hind quarters (Fig. 10), indicated for several weeks before she calved, that a cow was pregnant. Thus, it was obvious at the beginning of May 1961, that one of the Waterton cows, C.2, was pregnant, although she did not calve until 28 July. In other cases, particularly in young cows, the increase in size of the abdomen was not apparent. Shedding of the thick winter coat facilitated detection of pregnancy.

Another sign that a cow was in calf was the swelling of the udder. This occurred in all cases at least three weeks before calving, and in one case six weeks before calving. In three of the cows this was the only visible sign of pregnancy until a few hours before calving.

A further sign of pregnancy was the swelling and loosening of the vulva of the cow. McHugh (1958) noted swelling

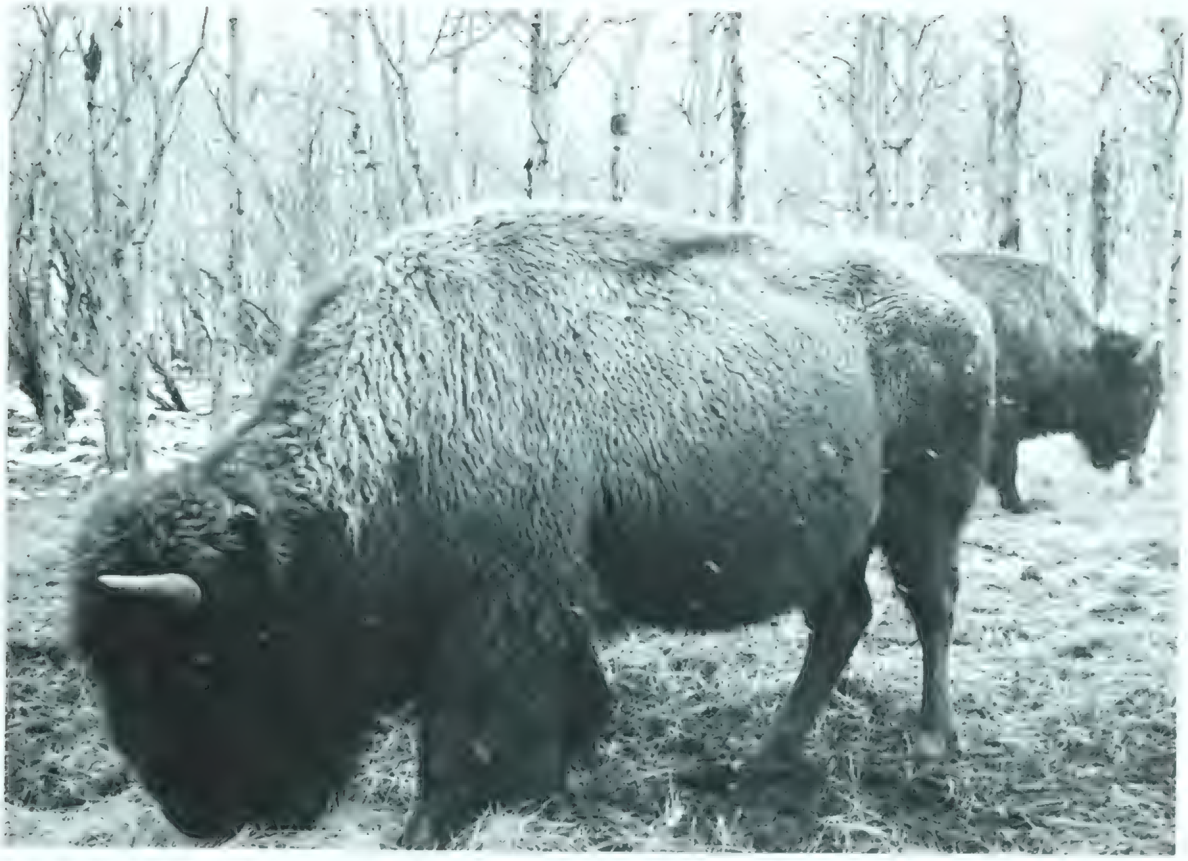


Fig. 10. Cow C.1, photographed three weeks before birth of her calf. Note rounded abdomen and hollow between abdomen and hind quarters.

of the udder and vulva of pregnant cows, but did not state how long before parturition this occurred. At first I thought that the swollen condition of the udder and vulva indicated that parturition would occur within the next few hours or days, but I found that a cow could remain in this condition for two or three weeks, and that it was not possible to tell when calving would occur until the behavior of the cow changed a few hours before parturition.

Up to 12 hours before calving, the cows became restless. As McHugh (1958) found, pregnant cows would make short trips away from the herd, and then return to it. I think this behavior showed a conflict between an urge to stay with the herd and one to leave it and be alone. McHugh found that some cows calved while in the cow herd. In the Waterton herd all cows left the herd to have their calves. It was noticeable that cows at this time were more than usually keenly aware of the presence of humans. Even though people were up to 400 yards away, these cows would constantly turn and stare at them, and move as far away from them as the limited size of the enclosure allowed.

Of the seven calves, two were born in the night, and five in the middle part of the day, either in the late morning or early afternoon. Four of the cows had their calves in the shelter of a clump of trees or in thick willow brush, and three calved out in the open. Of these latter three, one cow, C.10, went originally to a clump of poplar trees, but

left this place when I followed. Because of the hilly nature of the country, I had to follow the cow fairly closely, in order to be able to see her.

The Process of Parturition

My data on parturition, obtained from two cows, C.2 and C.10, in the Waterton herd, are summarized in Table II.

The process of calving in the two cases I observed in bison, seemed to be the same as in domestic cattle (my own observation). A discharge of thick mucus was followed by the appearance of the front feet of the calf, encased in the amnion, which soon broke, releasing amniotic fluid, and revealing the feet of the calf. Next, the calf's head appeared, and after a few minutes in one case, less than a minute in the other, the calf was born. The time between the beginning of the discharge of mucus, and parturition, was two and a half hours in one case, and four hours in the other. One cow, C.10, began to make trips away from the herd eight hours before the birth of her calf, the other, C.2, left the herd four hours before calving, but then returned, and finally left the herd only 20 minutes before calving. C.10 gave birth to her calf while standing up. The calf hung suspended, with its head and front half showing, for a few seconds before its hind end appeared and it then fell to the ground. The other calf was born a few seconds after the cow, C.2, (having finally left the herd where she had been walking about with the calf's feet protruding), lay down. It was

Table II. Summary of some data on parturition, obtained from two cows in the Waterton Park herd during summer 1961.

name of cow	C.10	C.2
name and sex of calf	*e*, male	*f*, male
birth date of calf	15 July	28 July
probable age of cow	3 years	more than 8 years
date and nature of first visible signs of pregnancy in cow	21 June swelling of udder	3 May or earlier rounded shape of body
hours before parturition when cow left herd	7	4 hours. then returned. finally left 20 mins. before parturition
hours between first mucus discharge, and parturition	2½	4
hours between the appearance of calf's feet, and parturition	½	1¾
place of parturition	in the open (cow originally made for cover)	in the open
position of cow at parturition	standing	lying
no. of mins. after birth during which calf motionless	6	3
no. of mins. between first standing attempts of calf, and standing up	10	4
fate of after-birth	probably not eaten by cow	eaten by cow

hard to see the labor strains when they occurred because both cows walked about continuously up until the moment the calves were born.

Both cows made periodic straining movements to get rid of the after-birth, which was hanging down to their heels. Six of the seven cows got rid of the after-birth within an hour or a few hours of parturition, but in one cow, C.4, it remained hanging for three days after the birth of the calf. I saw only one cow, C.2, eat the after-birth. It came away three and a half hours after parturition, and she turned around and began to eat it. C.10 shed the after-birth two hours after parturition and left it lying where it fell. It had gone the next day, so I do not know whether she returned and ate it or whether some other animal ate it during the night. I saw a crow pecking at it while the cow was still close by. I never found the after-births in the other five cases, so I assume that the cow or some other animal ate them.

Behavior of the Cow and Its Newborn Calf

As soon as their calves were born, the cows' behavior changed completely. Instead of walking away from an intruder, as they had done up until the moment of birth of the calves, they now stayed close to their calves, between them and any intruder. This behavior lasted until the calves were strong enough to follow. One calf, f, followed its mother, C.2,

in this way within 45 minutes of its birth. C.2 remained lying for a minute after her calf was born, then slowly stood up, turned around, and began to lick the membranes off her calf. C.10, which had been standing during the birth of her calf, slowly turned around, and slowly, apparently uncertainly, began to lick the calf's head region. The calves lay motionless for three to five minutes after they landed on the ground, and then began to raise their heads. Being licked by the cow apparently stimulated them to move. They seemed to direct their first movements towards the cow even before they could stand.

After three minutes in one case and six in the other the calves began to try to stand up. Their first efforts involved partial straightening of the front legs, and were followed by collapse sideways. Then they tried pushing up with the back legs after half straightening the front legs. They would then overbalance and topple forward on their noses or turn over in a somersault, or the hind legs would collapse so that they fell back onto the rump. They continued to make persistent efforts, however, and one stood up within 10 minutes of birth, the other within 20 minutes. McHugh (1958) quotes 18 and 20 minutes for two calves on which he had data, and K. F. Cooper told me (pers. comm.) that newborn calves he had watched in Wood Buffalo Park stood within a few minutes of birth. Jaczewski (1958) states that in European bison (wisent) Bison bonasus, the calves stand "immediately after

being born", and that reports to the contrary probably result from generalisations based on observations of pathological cases. It seems that bison calves stand much sooner after birth than calves of domestic cattle, which according to Brownlee (1950) try to stand up within an hour or less of birth, or according to Walker (1950) are able to stand within a few hours of birth.

Before they could stand, the calves made sucking motions in the air, towards their mothers. As soon as a calf was standing, its efforts were directed to suckling. The first suckling attempts of the bison calves were directed at the neck of the cow and then at the angle between her front legs and her body. The calves then appeared to follow the line of the cow's belly with their noses until they reached the angle of the hind legs to the body. They then quickly found the udder and sucked. The time between standing up for the first time and finding the udder was less than one minute.

During the first 30 to 60 minutes of life, the calves were licked almost continuously. They walked slowly and falteringly around the cows and suckled. While suckling they bunted vigorously at the udder, although this made them stagger on their unsteady legs. One cow, C.2, 45 minutes after the birth of her calf, walked away from me, followed closely by the calf. This calf was particulary strong, and ran bucking around its mother when only a little more than a

half hour old. C.10 and her calf lay down and rested, an hour after the calf was born.

From the moment of its birth until two or three hours later, a calf was in almost continuous physical contact with its mother. At first the cow licked it continuously, then it stood up and suckled and she continued to lick it. Then the calf staggered around its mother, touching her most of the time, and stopping every few minutes to suckle. In the next few hours the cow and calf alternated between periods of lying down resting; of the cow grazing close to her resting calf, returning to it frequently and licking it; and of the cow grazing with the calf walking or running in close circles around her.

First Contact of the Calf with Bison Other Than Its Mother

The new calf was an object of considerable curiosity to the rest of the herd. During the first few hours after parturition, the herd would come to the cow and calf and try to investigate the calf by sniffing and licking it. The individuals most interested in the calf were two- and three-year-old bulls, yearlings of both sexes, and cows that already had calves. These animals sniffed and licked the calf and also sniffed the cow. They frequently displayed the lip-curl posture and showed the gaping behavior (described earlier, p.14) after sniffing the calf or the ground where it had been lying or where the placenta lay. The cows tried to prevent

this investigation of their calves, by lunging after the other animals, or by making aggressive head-jerking motions at them.

I found that a cow's success in preventing this investigation was correlated with her position in the dominance hierarchy of the herd. The two highestranking cows, C.1 and C.2, were not bothered by the rest of the herd. Although the other bison came near them, few attempts were made to sniff either the cow or her calf, and the next day, these cows, with their calves, rejoined the herd of their own accord. The other five cows were joined by the herd "against their will". One of these five, C.12, the lowest ranking of the adult cows in the herd, had no success at all in keeping the other bison away from her calf, and was several times separated from the calf, which then tried to follow other animals instead of its mother. The remaining four cows, C.4, C.7, C.10 and C.11, had varying degrees of success in keeping the other bison from their calves.

It is an interesting problem, whether or not, in the wild state, a cow returns to the same herd that she left before parturition. If she stayed away two days it is quite likely that the herd she left would have moved away from the area in the meantime. Does a cow with a new calf join the nearest herd, even if it is a different one from the one she left, or does she stay quite close to her herd during the time she is separated from it?

In the Waterton herd, cows never stayed away from the herd longer than two days. This may be due to the small range over which the herd could wander, and it may be different in the wild. It is interesting to compare this behavior with that of other closely related species. Yermaloff (1906, cited in Glover 1947) stated that wild wisent cows in the Caucasus kept their calves hidden in thickets for six or seven days after birth before they rejoined the herd, but Glover thought this information was exaggerated because a calf born in a captive herd in Germany was seen to follow its mother at a gallop at three days of age. According to Mohr (1952), wisent cows stay away from the herd for three or four days after birth of the calf. In the Camargue cattle, (Schloeth 1961) behavior is different again. The cow leaves her calf alone, hidden, for the first three or four days, staying in the herd herself, and only returning to the calf to nurse it. After this time she apparently leads her calf back to the herd, where it joins a calf subgroup.

Discussion

Udder-seeking Behavior

Some behavior that I observed in calves of domestic cattle is interesting in connection with udder-seeking behavior of young ungulates. The calves were kept in individual pens, each of which had at the end furthest from the gate, a horizontal feeding trough, fixed from wall to wall across the

pen, about two and a half feet from the floor. Whenever disturbed, these calves would run to the trough, follow the line of the bottom of the trough with their noses, and make persistent bunting and sucking motions in the corner.

It has been shown in newborn ungulates of various species including goats, *Capra hircus*, (Blauvelt 1956), llamas, *Lama glama*, (Kraft 1957), giraffe, *Giraffa camelopardalis* (Lang 1955, cited in Thomas 1956) and domestic cattle (Adler, Linn and Moore 1958) that udder seeking behavior involves sucking motions directed at the angle formed between the leg and the body of the mother. Since this behavior is found in such young animals and is so stereotyped, it seems that it must be innate. This is confirmed by the behavior of the young domestic calves in relation to the trough, since they had never suckled from a cow. One aspect of this behavior, which Blauvelt (1955) discussed in connection with newborn goats, but which has not been emphasized, although it occurs in other ungulates, is the way the newborn animal follows the line of the belly of its mother until it reached the angle between the hind leg and the body.

Adler, Linn and Moore (1958) saw behavior similar to that which I described in the penned domestic calves, in adult cattle suffering from disturbances of the central nervous system associated with ketosis. They attribute this behavior to a reappearance, due to this disturbance, of a pattern of behavior that is normal in the young animal. In discussing

the tendency in a newborn lamb, Ovis aries, to follow along the mother's body when trying to nurse, they say that this is a "learning pattern of trial and error" and speak as though it were accident that the lamb's muzzle is "ultimately ... trapped in the ewe's inguinal region." I do not think that this is accident, nor, after seeing the behavior of the domestic calves, which had never suckled, do I agree that this behavior pattern is learned.

I think that a newborn ungulate has an innate tendency to search in the angle between a horizontal and a vertical surface on the cow. It searches first at the front end of the cow, probably because this is the nearest part of the cow at the time when the calf stands up, since the cow continuously licks her calf during its efforts to stand. Then it uses the line of the belly as a "guiding line" till it reaches the other corner. Once at the hind end, the calf probably finds the udder by its feel and by smell. I think the calves have to learn at which end of the cow the udder is, because I have seen calves up to a day old try to suckle behind the front legs of cow. Later than this, they went to the correct end.

The tendency of young ungulates to run to their mothers and suckle when frightened is well known. I think the domestic calves were displaying this tendency when they ran to the corner of the trough, -- they were using the trough as a substitute for their mother.

The Solitary Behavior of the Cow at Parturition

The tendency of cows to leave the herd before parturition, to stay away afterwards, and to prevent contact between their calves and the herd was so strongly marked and so consistent that there must be some reason for it. Probably the explanation is that during the time that the cow and calf are alone, a bond is formed between them, a kind of imprinting takes place, with the calf learning to recognize its mother by sight, smell and voice, without disturbance or interferance from the other members of the herd. If a situation occurred in the wild like that of the cow C.12, which got separated from her calf by the bison investigating it, it could lower the chances of survival of the calf, particularly if the calf were born in the cold weather of early spring. Probably then, there would be selection against behavior leading to this type of situation.

The close physical contact between the cow and her calf during its first few hours, and the fact that a calf suckles at frequent intervals during its first two or three days of life, are probably factors in the formation of the bond between cow and calf.

Behavior of the Cow and Calf after Rejoining the Herd

The Cow-calf Sub-group

In the Waterton herd, cows with calves stayed near one another, forming a cow-calf sub-group. Cows rejoining

the herd with newborn calves joined this sub-group, and cows with calves close to the same age showed a greater tendency to stay together than did cows whose calves were, for example, more than a month apart in age. The cows in this sub-group grazed and lay down close together, and the calves, following their mothers, were thus also close together. At first the cows alone were responsible for the existence of this sub-group, but later, the calves came to prefer the company of other calves to that of their mothers, and it became noticeable that calves grazed and lay near to one another rather than near their mothers. One of the cows in the Waterton herd stayed with the bull group until the birth of her calf, when she joined the cow-calf sub-group. When her calf was a month old, however, she began to graze with the bulls again, and from this time on, she was more and more often to be found with them. Her calf, however, stayed with the cows and calves, and the cow only returned to the calf to nurse it.

Activity of the Cow and Young Calf

Calves spent most of their first three or four days of life lying down. They suckled at irregular but frequent intervals for short periods of a minute or two. During the first two days, cows kept between their calves and other herd members, both when lying and particularly when grazing. When her calf was lying, a grazing cow would move in a circle or semi-circle or in a horse-shoe-shaped path around the calf

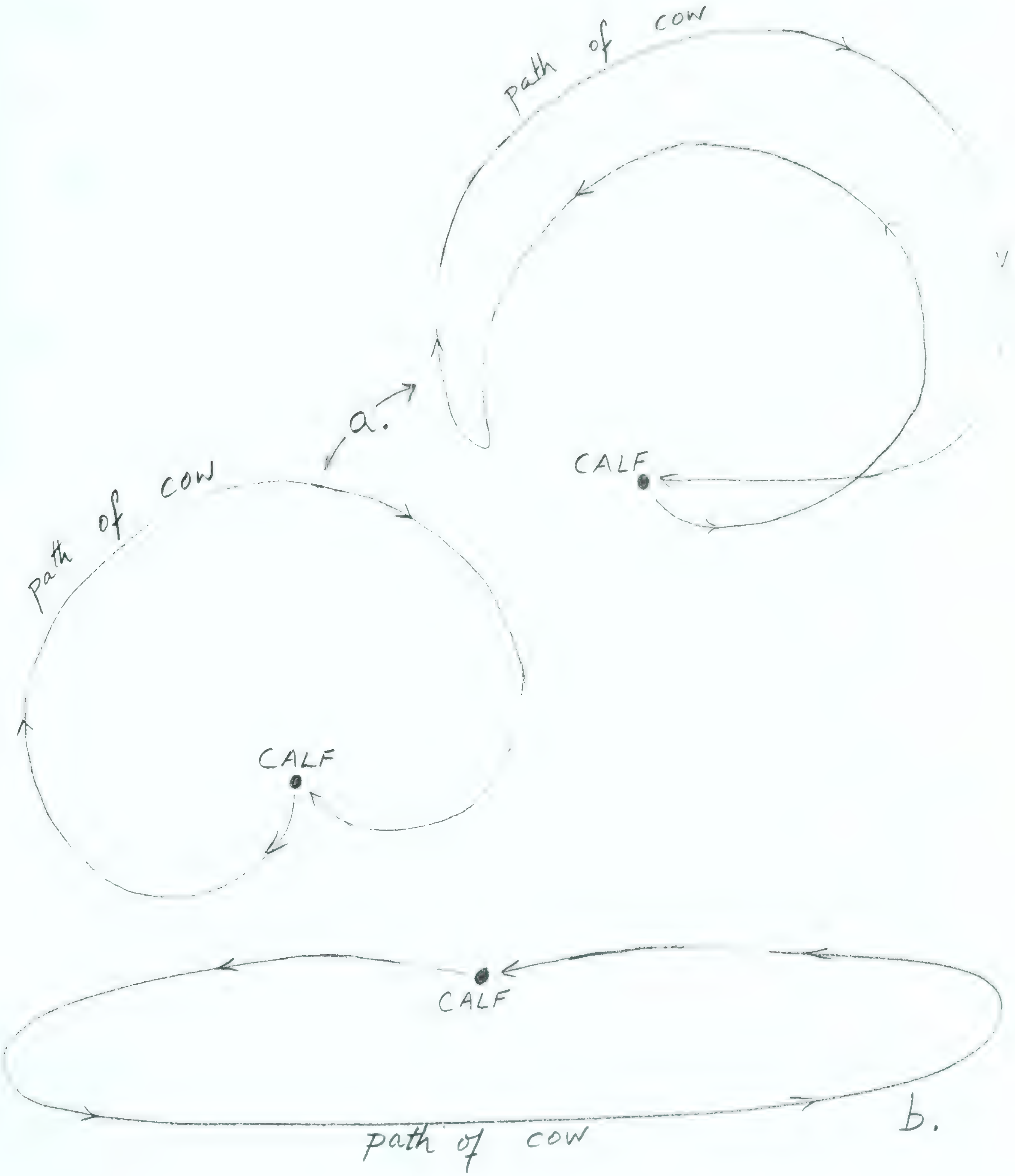


Fig. 11. Diagrams to show the manner in which a grazing cow moves around her calf.

a) newborn calf

b) calf two to five days old

(Fig. 11a) not more than about 15 feet away from it, and between it and other members of the herd. At frequent intervals, the cow returned to the calf and licked it. This usually resulted in the calf getting up and walking about a little and then lying down again in a different place. In connection with this habit of cows grazing in circles around their young calves, I should like to discuss a theory of Garretson's (1938), explaining the presence of circles of bare earth which apparently occurred on the prairies during the bison calving season. I quote from Garretson:

> "One of the strange sights on the prairies every spring soon, after the grass had sprouted, was the thousands of circles where the earth had been trodden bare. Early travelers, not knowing what caused them, called them "fairy rings". They were formed during the buffalo calving period. To keep off the gray wolves that singly or in great packs hunted over the prairies, the buffalo bulls formed regular beats to keep guard over the cows and walked around and around them, until circular paths were formed."

Surprisingly, this story appears to be widely believed, even by people with a fair knowledge of bison behavior. If these circles really existed, I doubt if they can have been connected with the actions of bison, unless the behavior of this animal has changed radically since the time of which Garretson speaks. For one thing, as Roe (1951) pointed out, the bison

bulls are in different herds, separate from the cows, during the calving season. For another, I have never seen bulls take the slightest notice of calves. The only interaction I ever saw between bulls and calves was when lying calves got up and moved out of the way of a bull that was walking past, or when a calf moved out of the way of a bull that was investigating the calf's mother. It therefore seems extremely unlikely that bulls would protect cows and calves from wolves. Although the normal reaction of a bison herd caught out in the open by wolves is to make a stand, closely bunched, ".... Other members of the herd, with the exception of the mothers of calves under attack, show no regard for the presence of the wolves" (Fuller 1960).

Another possible explanation of the trodden circles might be the behavior of the bison cow in grazing around her resting calf. However, the cow and calf are never in one place long enough for the cow to tread down the grass. As I mentioned before, the calf usually gets up and moves each time its mother returns to it and licks it.

There is an explanation in the behavior of bison for trodden patches of grass, but not for large circles. These trampled patches are caused by the cows during calving. If undisturbed, the cow stays in one place before parturition, and being restless, she gets up and lies down frequently. While standing, she walks about in a small area, and one cow in the Waterton herd flattened down four patches of grass in

this way. None of them were more than 15 feet in diameter, and they were all solid areas, not rings.

After the calf's first two or three days of life, its mother gradually stopped grazing in circles around it and would graze up to about 40 feet from it before returning to it. She would often go in a long oval pattern around it (Fig. 11b). In the third and fourth days of life a distinct pattern of behavior appeared in the calves. As the herd grazed along, the lying calves would begin to get left behind. As the herd got about 20 or 30 yards ahead, the calves would get up and walk after the herd, catch it up and lie down again. It was during this phase of following to catch up the herd that calves started to graze. Gradually they came to spend more and more of this time grazing, and only lay down when the rest of the herd was lying.

Play

The Nature of Play

It is characteristic of the play of animals that it is recognisable as such, and people will agree that an action is play, even though they may be unable to explain why they interpret it in such a way. Bateson (1955 and 1956) has put forward the important idea that this ability to recognise play as such is due to certain signals that the playing animals exchange. It is by these signals that the animals themselves "know that they are playing", and are able to dis-

tinguish play-fighting from the real thing, and playful nips from serious bites, and so on. These messages, which, in effect, mean to the animals "this is play", are messages about the subsequent actions of biting, chasing and so on, and are thus "messages about messages" or "metacommunication".

In bison calves, the actions most often seen before and during play, are bucking and gambolling and galloping around with the tail raised. Probably these actions give the message "this is play".

Play included galloping after other calves, tussling between calves, jumping over fallen tree trunks, touching strange objects and darting away from them, and use of a curious bounding gait like that characteristic of mule deer, Odocoileus hemionus, in which all four feet leave the ground at once (Murie 1954). Calves less than a week old galloped and bucked around their mothers. In a play-group the calves often galloped around for over half an hour with hardly a pause, and by the end would be panting with their tongues hanging out.

Solitary Play in Calves

Certain activities in calves less than five days old were classed as play although other animals did not participate, and were only indirectly involved. Bucking was first seen in a calf only 35 minutes old, as it ran falteringly around its mother. A few hours later this calf

galloped round the cow several times, until, appearing tired, it returned to her and lay down. At this stage it did not go farther than 15 feet from her, and kept returning to her and touching noses with her before galloping off again. The cow watched the calf all the time, following its movements by turning her head.

On its second day of life, a calf would gallop farther away from its mother, and investigate strange objects in its path. It would gallop in large loops and circles around the cow, up to 30 yards from her, always returning to her after each circuit, before galloping off again. It was at this time that a calf made its second type of contact with bison other than its mother. This contact occurred because a calf would sniff anything strange that it came across, including other calves, and occasionally adults. It usually darted back to its mother after briefly sniffing noses with the other animal. If this contact was just momentary, the calf's mother ignored it. If it was more prolonged, however, the cow would approach and the other animal would usually walk away. If it did not, the cow threatened it with a jerk of the head, or lunged after it.

Calves of this age and older, appeared to be intensely curious and not at all afraid. I often saw them run after and sniff bison their mothers had just driven off. They began to investigate new objects more thoroughly, picking up sticks and stones in their mouths and dropping them again, following cowbirds, Molothrus ater, and other animals (including on

one occasion two jack-rabbits, Lepus townsendi, and on another, two mule deer bucks.) On 1 August I saw two calves investigating water, probably for the first time. One calf was two days, the other four days old. They walked along the shore of a lake, splashing in the water, mouthing it, trying to pick it up, and shaking their heads and ears. Then they ran out of the water and one returned to its mother. Then they went back to the water again and one ran through a flock of cowbirds on the shore, splashing, and jerking its head at them. After this it ran, bucking and tossing its head, back to its mother. The older calf ran to the shore and rolled in the sand before returning to its mother. This return to the mother after the first brief contact with something new, followed by return to the object again, has been seen in other young animals, particularly monkeys (Harlow and Zimmermann 1959). The mother is treated as a "base" from which to explore and investigate. Whenever it is frightened, the infant runs back to its mother.

Play between Calves

Play usually took place during a grazing period towards the evening, when the activity of the herd was highest but it also occurred occasionally during the day at any time of activity in the herd.

On one occasion I saw a two-year-old cow try to play with two calves, and another time a yearling tried to

play with calves. In both cases the calves ran away from the older bison. Apart from rare play interactions between older animals, all other play involved only calves.

Calves less than a week old did not play with other calves. If older calves approached a young calf and tried to play with it or investigate it, its mother would walk towards them and the older calves would run away. After about a week, the mother of young calves began to tolerate play contact between her calf and other calves. The younger calves in a play group usually stopped playing before the older ones did, and returned to their mothers to suckle or lie down.

Invitation to Play

On five occasions I saw an interaction that appeared to be an invitation to play, made from one calf to another. Four times one calf that was playing, galloped to another which was not, and looking at it, ran bucking past it. The second calf then chased the first. Once a calf walked up to one that was lying down, and standing over the lying calf, it wagged its head in a circular motion, or jerked it up and down vertically. The lying calf did not stand up, however, and the first calf walked off. This head wagging motion appeared to be the same as that seen in the play-fighting of young bulls, and described earlier. In four of the five cases the calf giving the invitation was the older

of the two. Only once did a younger calf try to make an older one stand up in this way, and when the older calf stood up and ran after the younger, the latter ran off to its mother.

Play-fighting in Calves

Part of the play of calves and young bulls was a form of fighting. This fighting is considered as play because it contained and alternated with some elements of play, including bucking, kicking and galloping between bouts of fighting. It contained none of the elements of fighting behavior of adult bulls except pushing with foreheads together.

Play-fighting in calves consisted of butting and pushing with the heads together. Often the calves' heads would slip apart because their horns were so small. In older animals the horns were usually locked with those of the opponent, one set above the other, during play-fighting.

Table III shows the number of times that individual calves were involved in play-fighting interactions, and which calf won each interaction. Wins and losses were assessed by seeing which animal backed the most or by which one turned away from the other or ran off.

From the tendency among the younger members of the Waterton herd, for older animals to dominate younger ones, one might expect that the older of a pair of calves would be the winner of play-fighting interactions. In 13 of the 29 interactions, this was the case. In 10 cases, however,

Table III. Play-fighting interactions between calves

		LOSERS							
	name and sex of calf birth date of calf	a	b	c	d	e	f	g	total wins
WINNERS	a, male born 14 May		4		6				10
	b, male born 23 May				1				1
	c, female born 5 June		2		1	1			4
	d, male born 15 June			6					6
	e, male born 15 July								
	f, male born 28 July			1					1
	g, male born 30 July					1			1
	total losses	0	6	7	8	2	0	0	

the winner was the younger calf, and on 6 occasions, no winner was recorded. These 10 cases when the younger calf was the winner, can be explained. Seven of the 10 interactions involved a female calf losing to bull calves younger than she was. In the other three cases, the mother of the younger calf was nearby, while the older calf's mother was some distance away. I think that this affected the result of the fight, although the cow actively interrupted only one of these encounters. Except with female calves then, the result of a play-fight is usually that the older wins and the younger loses.

Probably it is as a result of these play-fights that dominance relationships are first formed in calves. Within the yearling and two-year-old age-groups, as already mentioned, bulls were dominant to females. It appears that this tendency was already present in calves.

Bateson (1956) has pointed out that in play, human children learn not only to act different roles, but much more important than this, they learn that such roles exist. This is probably also true in animal play-groups, including those of bison. Not only does a young calf learn to be dominant or subordinate, but it learns that such distinctions exist. In a species in which the stability of the social group probably depends upon the existence of a dominance hierarchy, such a learning process would be most important not only for the survival of the individual, but also for

the existence of the society.

Mounting Behavior in Calves

Mounting behavior often occurred out of the context of rutting behavior, as part of the play of calves and young bulls. It is included with play rather than with sexual behavior because of its frequent association with play-fighting and because it lacked any other elements of rutting behavior. Of the 24 occasions on which I saw mounting behavior in calves, 11 also involved play-fighting.

Calves were only involved in mounting interactions with bison of other age-groups on three occasions. On one occasion a female yearling mounted a calf, and two other cases involved male calves, five and ten weeks old, trying to mount their mothers. With these three exceptions, calves took part in mounting interactions only with members of their own age-group.

Table IV shows data on mounting behavior in the four oldest calves in the Waterton herd. (I have no data for the younger three, two of which were only two weeks old and one, four weeks old when I left Waterton). In discussing mounting behavior, I shall refer to the animal that mounted the other as the "mounter" and to the animal that was mounted as the "mountee". Of the 23 occasions in which calves took part in mounting interactions, 14 involved the older calf as mounter and the younger as mountee. A calf mounted

Table IV. Mounting behavior in calves

calf[*]	sex of calf	numbers of times as "mounter"	number of times as "mountee"	number of interactions in which role alternated	total number of times involved
a	male	12	5	4	21
b	male	8	7	4	19
c	female	0	2	0	2
d	male	2	6	0	8

[*] Designation as in Table III

an older one five times and there were four occasions on which they alternated roles during one interaction. Considering the 19 single interactions, the mounter was the older calf 14 out of 19 times, or 73.6 per cent of the time. The 95 per cent confidence limits for this binomial are 47 per cent and 91 per cent. The probability of the mounter being the older calf 14 or more times out of 19, by chance alone, is 0.031. Note that the female calf was never seen to mount another calf, although she was mounted on two occasions by a male calf. The youngest age at which a calf was involved in a mounting interaction was six days. Except for the oldest calf in the herd, a calf was always mountee during its first mounting interaction.

On four occasions, mounting interactions between calves were interrupted by older members of the herd. On one of these occasions three older animals were involved. In each case, the older animals approached the calves and made head-jerking threat motions at them. The calves then moved off in different directions. The bison interrupting this mounting behavior were usually young animals. The mother of one of the interacting calves was involved once, a three-year-old cow once, a two-year-old cow once, two-year-old bulls twice, and a yearling once. I do not know what significance, if any, this behavior has.

The Significance of Play

I have discussed one of the functions of play in

connection with Bateson's idea about learning the existence of different roles. Some of the other theories of play have been summarised by Beach (1945). Three of these may help to explain the significance of play in bison.

One of these theories suggests that play may encourage certain inter-individual reactions that may be of importance to the species. The social integration of bison calves (discussed in more detail later) involves two important processes, the development of the calf's behavior so that it comes to resemble that of adults, and the loosening of the bond between the calf and its mother. I think that play in bison calves accelerates both these processes. Almost all a calf's interactions with animals other than its mother, are with other calves. Play is the main form of interaction between calves. Play leads to behavior such as mounting, fighting and wallowing, all of which are first seen in a play context. Thus, I think it can safely be said that play hastens the development of behavior of the calf. In addition, from the time that a calf begins to play with other calves, it gradually comes to prefer the company of the other calves to that of its mother. Thus play also helps to loosen the bond between a calf and its mother. This shows the importance of play in the social integration of calves.

Another theory of play suggests that it is a means by which a young animal explores its own capabilities, and

becomes familiar with its environment. I think that this is the significance of some play in bison calves. I have described how calves only a day or two old would gallop around their mothers in large circles, stopping to investigate strange objects, and darting back to their mothers again. This trait continued in the play of older calves. I think it is safe to assume that there would be a selective advantage in a young animal becoming familiar with its environment in this way, particularly while it is still under the protection of its mother.

Perhaps the most popular explanation of play is that by it an animal practises patterns of behavior which become important in adult life. This theory is supported by the fact that in their play, the young of widely different mammal species all show in incomplete form, behavior which is of survival value to the adult in the wild state. While I would prefer not to use the word "practice", since I think it implies some conscious effort on the part of the animal, I do think that the galloping, racing, chasing and fighting games played by young bison could be of value to the animal later, and thus the tendency to play in this way would have a selective value. Meyer-Holzapfel (1956, cited in Altmann 1956) has pointed out that in general, the play of young ungulates centers on the topic "flight". This is true also of bison, as I have described. Probably this type of play is valuable in improving muscular control and

coordination. In ungulates, whose main defence in the wild state is flight, such muscular control and coordination could be important to the survival of the animal. However, as Beach (1945) pointed out, in order for this theory of play to be acceptable, it must be proved that the adult performs more efficiently the actions it is supposed to practise, if it is allowed to play as an infant, than if it is prevented from playing.

It has not been proved that the coordination of the adult is improved by the running games of the calf. Play is important in the social integration of the calf, however, and also in the exploration of the animal's environment. Because these results of play are important to the survival of the adult animal in the wild state, the tendency in the calves to play in these ways has a selective advantage.

Vocal Communication between Cow and Calf.

Cows and calves can communicate with one another over a long distance. This communication is by means of a deep belching grunt. In calves the sound is higher in pitch and more nasal in quality than in adults. I could detect some variation in the tone between individual adults. Apparently wisent cows and calves also communicate by means of a grunt (Jaczewski 1958). Schloeth (1958a) reported that cows and calves of the Camargue cattle each have two sounds for vocal communication. Cows have a moo and a grunt and the calves have a bleat and a grunt. The moo and the bleat are used over long distances, while the grunt is used for communication at close range. Domestic cattle, as far as I know, do not grunt, but the cow, when close to her calf makes a characteristic lowing sound (Brownlee 1950). At greater distances the domestic cow and calf communicate by means of a moo and a bleating sound. It appears that the Camargue cattle are intermediate between bison and domestic cattle, in this respect.

Deakin, Muir and Smith (1935) reported that the grunt heard in bison cows and calves is the same sound as that heard from bulls in the rutting season. Schloeth (1958a) stated that the grunt of the cow and the roar of rutting bulls are the same in Camargue cattle, and Jaczewski (1958) reported that the bellow in wisent bulls is similar to but

deeper than the sound used by cows and calves. I have no data on these latter species, but I do not agree that the grunt and the roar in bison are the same sound. The grunt is a belching sound, produced in the throat with the mouth closed. The roar of a bull in the rutting season is produced while breathing out, with the mouth open and the tongue out. It is more prolonged and much louder than the grunt, and the quality of the sound is quite different.

Deakin, Muir and Smith (1935) reported some interesting results of cross-breeding experiments with bison and domestic cattle. The bison-domestic females grunt, apparently, although the sound may be more prolonged than the normal grunt. Three-fourths bison females grunt like pure bison. Some hybrid males make a bellowing sound similar to that of domestic bulls, and one-quarter bison hybrid bulls bellow like domestic bulls. These authors think that the grunt is controlled by a pair of factors which exhibit incomplete dominance in the female with a further modification towards the domestic-type voice in the male. They seem to be assuming that the grunt, and the roar of rutting bulls are controlled by the same factors. Domestic calves raised by bison cows were afraid of the grunt of their foster mothers, but later became accustomed to it.

The grunt in bison is used by any member of the herd but only very rarely by adult bulls. In animals other than cows and calves, it is heard when the herd has been split

up, or when the herd is disturbed by humans, and sometimes from bison in the herd when one member of the herd has wandered off alone. On one occasion, shortly after the birth of a calf in the Waterton herd, this calf and its mother, plus another cow and calf were lying together about 200 yards away from the rest of the herd. A two-year-old cow and a yearling began to gallop back and forth between the cows and calves and the main herd, grunting as they went. Sometimes I heard bison grunting when the herd was in a stand of trees. Under these circumstances I could not tell which animals were grunting, but it was not only cows and calves. From these data it appears that the grunt probably functions as a warning call and as a means of keeping the herd together.

I never heard anything corresponding to the "threat grunt" described by McHugh (1958), even when bison were being herded around in a corral.

Cows and calves grunted to one another when they become separated in a herd movement, or if a calf failed to get up and follow when the herd moved off to graze. Cows and calves often grunted when they were relocating one another prior to nursing as the herd was moving off to graze. In these circumstances cow and calf grunt back and forth alternately.

McHugh (1958) gave evidence that a cow and her calf can recognize one another individually by means of this grunt. I also have data showing that this is the case. At the

roundup and branding in Elk Island National Park in November 1961, I had the opportunity to watch the behavior of cows and calves that were separated in different corrals, and after they were released into the same corral. While separated, cows and calves kept up a continuous grunting. They showed what apparently was searching behavior, walking up and down along the fences, looking around. On being released into the same corral, the cow or calf would gallop about among the bison already there, grunting, and within seconds the other member of the pair would emerge from among the other animals and gallop towards the newly released animal. Sometimes the pair briefly sniffed noses as they met, but usually the calf ran straight to the suckling position. Calves did not often actually suckle in these cases, or if they did, it was very brief. As the pair approached one another, there were usually too many other animals in between them for them to be able to see one another, so I can only assume that they could recognize each other by the grunt. Under natural conditions, it was common to hear a cow grunt to her calf and for only the correct calf to respond, although there were several others nearby. This sometimes happened in circumstances where the cow and calf could not see one another, so it seems that grunting alone is sufficient to enable cow and calf to recognize one another.

Sometimes a calf would not respond immediately when its mother called it by grunting. The cow would grunt in the

direction of her calf which was lying flat on its side, presumably sound asleep. The first few grunts might produce no result at all. Then the calf would half raise its head, and let it fall again. Gradually the cow's persistent grunting would result in the calf raising its head, looking at her, slowly getting up and slowly, as though reluctantly, following its mother. On one occasion a cow whose calf remained lying after the herd had moved off to graze, started to follow the herd herself, after her grunting to her calf had had no result. Within a few seconds of the cow leaving to follow the herd, the calf jumped up and galloped after her.

Differences in Behavior between Adults and Calves

Certain behavior patterns of adult bison did not appear at all in calves. These included roaring, fighting, and sequences such as horning, wallowing and pawing. (This behavior is discussed in the section of the rut.) Other behavior of adults was shown in calves, but was different in some way in calves. Included in this category were the processes of standing up, lying down, wallowing, the lip-curl posture, and mounting behavior.

Standing up

The motion of standing up consists in adults of three movements, -- lifting the weight of the trunk off the ground and putting the weight on the knees, raising the rump off the ground and straightening the hind legs, and lastly,

straightening the front legs. (Garretson's statement, 1938, that bison bulls rise in the same way as horses, straightening the front legs first, is not correct.) In bison calves, the process of standing up consists of a single motion -- all four legs are straightened at once and the calf appears to bound up. Adult bison rise in this way when alarmed, as Garretson (1938) noted. By the time a calf is four weeks old, it gets up in the same way as adults normally do.

Lying down

The process of lying down in adult bison is the opposite series of movements to that of standing up. First the animal kneels down on its front knees. Then it moves its hind feet forward and slowly puts its weight on its rump, on the ground. Finally it lets its weight off its knees, onto its chest on the ground. Young calves appear to be unable to perform this series of movements, and for the first two days to the first week, (there is some variation among individuals) they bend their front legs, and then appear to fall forward onto their chest or chin and end up in the lying position. As in standing up, the process seems to be one movement, but in this case the calf appears to fall into position because it is unable to balance while performing the actions in order, as adults do. McHugh (1958) briefly mentioned this characteristic of young bison calves, and Brownlee (1950) noticed the same thing in domestic calves.

After a few days to a week, calves were able to lie down slowly in a coordinated manner, as adults do.

Wallowing

McHugh (1958) noted that "wallowing among calves, first seen at the age of 13 days, lacked the skill of adult wallowing for at least the first month". In the bison that I observed, wallowing differed from the adult behavior until individuals were at least a year old. In adults, wallowing is performed vigorously. A series of powerful strokes with the legs nearest the ground pushes the upper pair of legs well into the air, and causes the shoulders and hump to hit the ground with an audible thump. In calves, which were first seen wallowing at the age of four days, there is no such push of the legs against the ground, and wallowing consists more of a wriggling motion of the body, with the legs waving in the air. The process appears to lack coordination. Even in yearlings there was not the same vigor in wallowing as there was in adults.

I never saw bison older than calves roll right over when wallowing, as horses, Equus caballus, do. Garretson (1938) stated that "The animal's hump seems to offer no obstruction whatever; he will curl himself up and roll over as quickly and apparently with as much ease as a mule." I think that this statement, except as applied to calves, is incorrect. The hump, particularly in bulls, is too prominent to allow the

animal to roll over.

Although the actions of pawing the ground, horning it, rubbing the chin and wallowing were all seen performed separately in calves, yearlings and two-year-olds, they were only seen performed in sequence in adult cows and bulls. Perhaps the sequence only becomes significant in adults, because of the importance of the sequence in threat behavior (discussed later).

The Lip-curl Posture

The lip-curl posture (Fig. 16) has been described in an earlier section. Table V shows data on the occurrence of this behavior pattern in calves. It was observed in the four oldest calves in the Waterton herd, a total of 22 times. Calf *c*, a female, did not show the behavior pattern at all. The youngest calf to show the behavior was ten days old at the time.

One difference between adults and calves was in the time for which the posture was held. For seven occasions on which the duration in calves was noted, the average was 6.9 seconds, while in adults, the posture was almost always held for at least 10 seconds, and occasionally for as long as 15 seconds. The posture was also less pronounced in calves than in adults, and was held less steadily. In two-year-olds the behavior seemed to be the same as that in adults.

The most common situation in which this behavior is

Table V. Lip-curling in calves

calf	number of times seen	age (in days) of calf when behavior first seen
a	10	19
b	8	15
c	0	--
d	2	28
e	2	10

seen is just after a bull has sniffed a cow. I only saw a calf sniff another animal and then show the lip-curl on three occasions. In one case a calf sniffed its mother; another sniffed a cow that had calved a few hours previously, and on one occasion a calf sniffed another calf. On all the other occasions, the lip-curl occurred when a calf sniffed an object or the urine of another bison on the ground.

Mounting Behavior

Mounting behavior occurred as play in young bulls as well as in calves. Certain differences existed between the age-groups, in this behavior. In calves, the mounter, except in the case of female calves, was usually the older of the pair. I did not know the exact ages of the young bulls, but the role of mounter or mountee was not consistent within any one pair.

In calves, the relative position of the two animals was often different from that seen in mounting occurring as part of sexual behavior. A calf would often mount from the side of the other animal instead of from the posterior. In young bulls, mounting was usually from the normal posterior position. Erection of the penis and pelvic thrusts sometimes occurred during mounting behavior in young bulls, but were not seen in calves.

Mounting behavior of calves also differed from that of young bulls in that the bulls often had prolonged mounting

sessions, with two animals taking turns mounting one other, while in general, mounting interactions between calves were short, lasting only a minute or less. Calves a and b occasionally had more prolonged mounting periods. They were the oldest of the seven calves, so perhaps this shows a development in behavior from the brief mounting interactions of younger calves.

Suckling Behavior

Occurrence

Calves less than about three days old suckled at frequent, irregular intervals, and each suckling period was short, lasting only two or three minutes. Sometimes, several of these short suckling periods occurred within an hour. Later, a rhythm appeared in the activity of the calf, and suckling only occurred three or four times a day. The times of day when suckling usually occurred -- and several calves could often be seen suckling at the same time -- were between 8:00 and 9:30 a.m., 3:00 p.m. and 5:00 p.m., and 7:00 and 8:30 p.m. The first two peaks in suckling activity occurred as the herd moved off and began to graze after a resting period. The third was during the evening grazing period, at the time when play and general activity were at their highest. Similarly, in calves of the Camargue cattle, most suckling was as the herds moved off and began to graze (Schloeth 1958a).

Calves also suckled at any time when they were frightened or disturbed, as for example when a car was driven near the resting herd. If this disturbance occurred close to a time when the herd would have moved off even if there had been no disturbance, a general suckling period with most or all of the calves feeding, would usually follow. Otherwise, only the calves nearest the source of disturbance would suckle, and the suckling time would be shorter.

Duration of Suckling

Table VI shows data on the duration of suckling periods for the seven calves in the Waterton herd. The columns correspond to the number of weeks after birth of the calf. Calves over three months old, as well as very young calves, suckled for shorter periods than those of intermediate age. This does not show up in the table, probably because I do not have a sufficient number of exactly timed observations of suckling. On the few occasions in Wood Buffalo Park (1961) and in Waterton (1962) when I saw yearlings suckle, the duration of suckling was not more than three or four minutes. The time range for suckling was from a few seconds to 15 minutes. The overall average, shown in Table VI, was 6.7 minutes. It seems that suckling time varies widely among different ungulate species. Schloeth (1958a) gives ten minutes for the Camargue cattle. For domestic calves, Walker (1950) gives 2 minutes to 25 minutes feeding with between 10 seconds to 10 minutes

Table VI. Average suckling times, in minutes, of seven bison calves, during successive weeks after their births. Waterton Park 1961.

calf	Number of weeks after birth 1	2	3	4	5	6	7	8	9	10	11	12	13	Birth date of calf
a	5.1 n=6	6.3 n=6	6.2 n=9	6.2 n=9	8.8 n=2	7.0 n=2	6.0 n=2	7.8 n=4	5.2 n=3	7.0 n=5	6.4 n=4	8.2 n=5	5.8 n=3	14 May
b	7.5 n=7	6.7 n=5	8.6 n=7	7.6 n=4	8.8 n=2	6.5 n=1	8.2 n=5	6.0 n=1	8.3 n=3	4.2 n=2	5.0 n=2	5.5 n=2		23 May
c	7.2 n=8	6.8 n=4	3.0 n=2	4.4 n=4	6.8 n=4	6.5 n=2	4.8 n=3	9.0 n=2	- -	7.3 n=3				5 June
d	6.7 n=4	1.5 n=3	3.0 n=2	6.5 n=3	5.2 n=3	7.1 n=4	- -	5.5 n=2	2.0 n=1					15 June
e	9.5 n=2	7.0 n=3	6.3 n=3	9.4 n=4										15 July
f	7.6 n=3	7.5 n=4												28 July
g	4.7 n=6	10.0 n=2												30 July
weekly average	6.6 n=36	6.3 n=27	6.4 n=23	6.7 n=24	7.1 n=11	6.9 n=9	6.7 n=10	7.4 n=9	6.1 n=7	6.5 n=10	5.9 n=6	7.4 n=7	5.8 n=3	6.7 n=182

actually suckling. In calves of caribou, Rangifer arcticus, the duration of suckling is far less. de Vos (1960) stated that suckling lasts from a few seconds to 3 minutes, with an average of 30 seconds. I do not have data to show the time of feeding compared with that spent actually suckling. However, in undisturbed calves more than a day or two old, the whole feeding time appeared to be spent suckling without a pause.

Position of the Calf while Suckling

In the great majority of cases, the calf stood parallel to the cow but faced in the opposite direction to her while suckling (see frontispiece). This is the normal position for nursing in most ungulates. In this way the calf is in close physical contact with the cow during nursing. Sometimes a cow would shift around in a circle, or move forward while her calf was suckling, and the calf often maneuvered then without stopping suckling, in order to remain parallel with the cow. Sometimes, when a cow moved forward and began to graze before her calf had finished suckling, the calf would continue to suckle, but from behind her, through her hind legs. Schloeth (1958a) observed the same behavior in the cows and calves of the Camargue cattle. Walker (1950) saw domestic calves suckle in this position, but does not mention whether or not it was the result of the cow moving forward. Unless disturbed, calves usually suckled on one side of the cow for

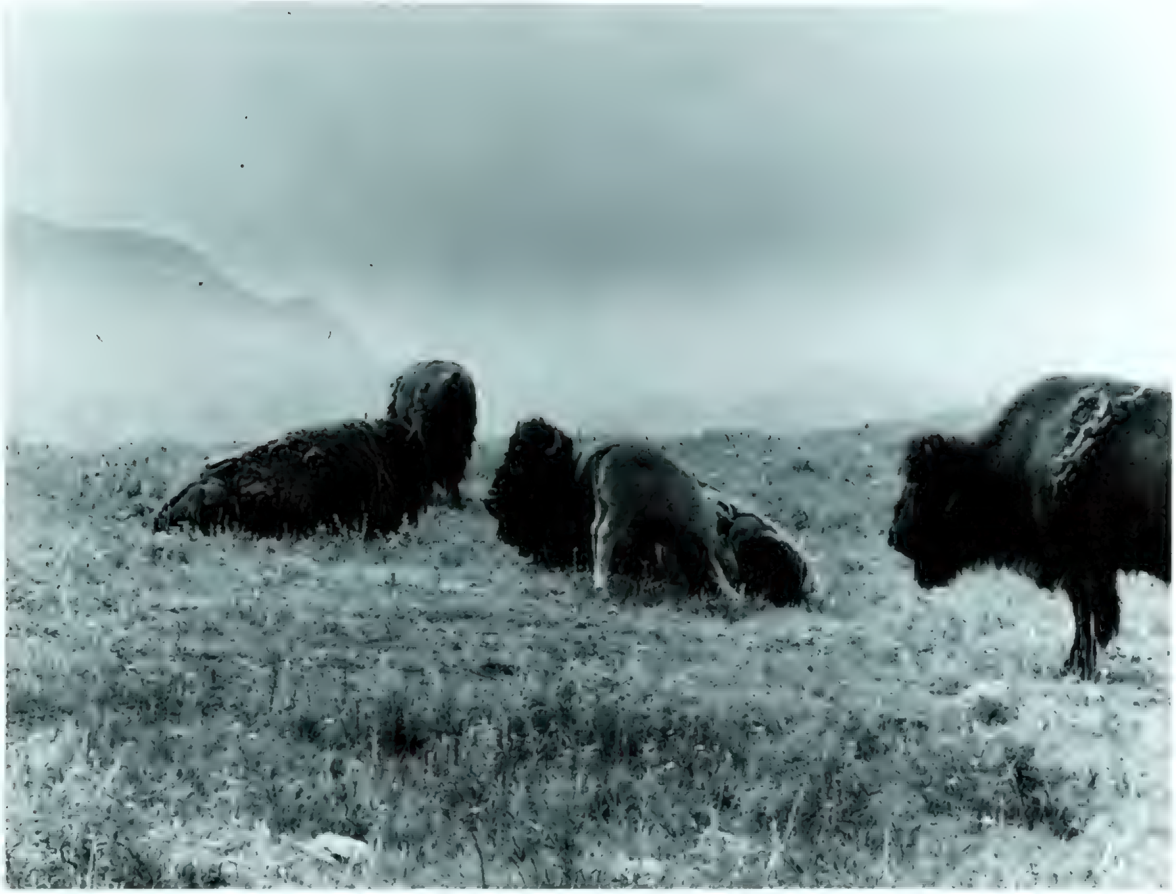


Fig. 12. Cow remains lying while its calf suckles.

the whole of any one suckling period. The same thing is the case in Camargue cattle (Schloeth 1958a). According to Walker (1950) the behavior of domestic calves in this respect depends on the size of the cow's udder. If the udder is small, so that the calf can reach all four teats from one side of the cow, it will suckle on one side only.

One of the calves occasionally suckled, or attempted to suckle, while its mother was lying down (Fig. 12).

"Heading-off"

When disturbed by the cow moving forward during suckling, calves employed a behavior pattern referred to here as "heading-off". As the cow walked forward, the calf would get left behind. It would then run after its mother, catch up with her, and then run around under her neck, pressing hard against her chest as it went. This usually stopped the cow. In the next second, the calf would be back in the suckling position, on the side opposite to that on which it had previously been suckling. If the cow did not stop walking when the calf ran around her the first time, the calf would repeat the maneuver until she did stop.

This behavior serves most effectively to stop the moving cow, and also enables the calf to regain the nursing position. I do not know whether domestic calves show this behavior, but Schloeth (1958a) observed it in calves of the Camargue cattle. Apparently these calves develop the behavior

gradually over a few months, unlike bison calves which do it from their first day of life. I saw a bison calf only 45 minutes old show this behavior pattern.

Calves Inducing Their Mothers to Stand

Certain behavior patterns of the calves usually resulted in the cows standing up. Whenever a cow stood up, following this behavior, the calf always attempted to suckle. This behavior was seen on 22 occasions. It consisted of the calf approaching the cow and laying its chin on her back. This was often followed by the cow standing. If the cow did not stand, the calf walked around her, butting its head against her side and sometimes pushing its head against hers (Fig. 13).

There were two situations in which this behavior occurred. One was when a cow lay down while its calf was suckling. The other situation was when a calf had not suckled for some time. The calf would approach its mother as she was lying resting, and induce her to stand. As Table VII shows, cows were induced to stand 15 times, with the calf suckling on 13 of the 15 occasions. Seven times out of the 22, the cow remained lying. These latter cases were when the cow lay down while the calf was suckling. I never saw a cow that had lain during nursing, stand up again and let the calf continue suckling. As Table VII shows, one calf, a, showed this type of behavior more often than the others did. Its mother, C.11, was more inclined to terminate a suckling period by lying down, than the other cows were. This explains

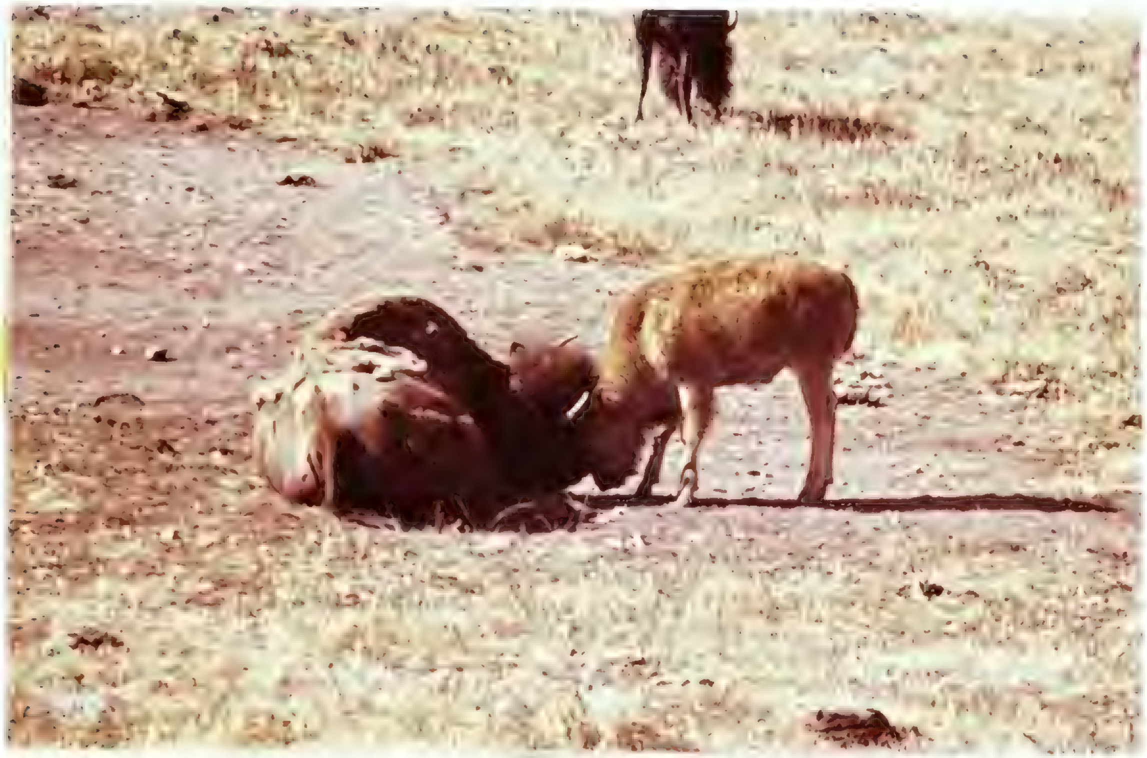


Fig. 13. Calf butting its mother.

Table VII. Attempts by calves to induce their mothers to stand.

calf	cow stood up and allowed calf to suckle	cow stood up but did not allow calf to suckle	cow lay during suckling and would not get up again
a	6	1	6
b	1	1	
c	1		
d	1		
e	3		1
f	0		
g	1		
total	13	2	7

the six occasions when calf a could not induce its mother to stand. The 13 cases where cows stood up and permitted nursing were all when this butting behavior by the calf preceded nursing; i.e., a calf that had not suckled for some time approached its mother and induced her to stand up. Thus, a cow was more likely to stand up if the calf had not just been suckling.

Variations in Suckling Behavior

Several differences in suckling behavior existed between individual cows and calves.

One of the calves, e, suckled from behind its mother, through her hind legs, far more often than any of the others did. On several occasions this calf was seen walking along behind its mother, nursing as she walked along. This calf did not show heading-off behavior until it was about a week old, and later, if its mother walked forward during suckling, it often suckled through her hind legs instead of showing heading-off behavior.

Calf a, on the other hand, was more persistent than the other calves in showing heading-off behavior. Perhaps this was partly because its mother, C.11, more often walked forward during nursing than did the other cows. As Table VII shows, calf a more often showed the behavior used to induce its mother to stand, than the other calves did. This calf was also the only one that attempted to nurse while its mother was lying. In the case of the cow C.1 and her calf, b, the

situation was reversed. Calf b seldom showed heading-off behavior, or suckling through the cow's hind legs. This cow would usually stand still for seven minutes or more while b was suckling, and then abruptly and decisively walk forward. The calf would then run after her, but seldom tried to continue suckling.

Weaning

Weaning in bison is a gradual process, lasting over several months. McHugh (1958) observed cases where calves followed their mothers for over a year. He found that aggression between a pregnant cow and her yearling-calf were rare before the birth of the new calf, but were frequent after its birth. He noted that cohesion between calves of 8 to 12 months of age and their mothers was still close enough for identification of the pair at most times. In the Waterton herd, in early May 1961, I could find no clue as to which cows were the mothers of two yearlings that were born on 12 June and 2 July 1960. The two yearlings behaved as independent members of the herd. At the round-up and branding in Elk Island Park in late November 1961, it was possible to identify all the calves with their mothers, although the calves were about seven months old by that time.

McHugh (1958) observed eight instances of yearlings suckling, and found that the duration of suckling was between two and eight minutes with an average of four minutes. I saw yearlings in Wood Buffalo Park suckling, on a few occasions,

and the duration was never more than four minutes. Neither McHugh nor I saw cows show any aggression towards the yearlings in these circumstances, and the yearlings were allowed to suckle until they stopped of their own accord. The yearlings I saw were large and strong enough to push the cows sideways as they suckled. Two calves in the Waterton herd, born on 31 August and 1 December 1961, were both seen suckling on 1 September 1962, when they were 9 and 12 months old respectively.

Fuller (1962) found that of a sample of 105 cows killed in January 1952, in Wood Buffalo Park, 33 per cent were still lactating. The calves of at least some of these cows were presumably born during the normal calving season, i.e. May and June of the previous year, and would thus have been eight or nine months old in January.

It appears, then, that it is usual for bison calves to suckle until they are nine months old, and in some cases yearlings continue to nurse if their mothers do not have new calves. Probably, in the wild, cases of calves continuing to suckle right up to the time of birth of a new calf are rare, and calves probably stop nursing some time between nine months and a year of age. Bison cows do not appear to force-wean their young, as some other mammals do, although it is possible that in the wild, pregnant cows show aggression towards their yearling calves during the three months preceding the birth of the new calf. Observations on wild bison during this time of year are not extensive enough to prove whether or

not this occurs.

I have discussed, in the section on the rut, behavior of cows which may accelerate the weaning process.

DISCUSSION

The Social Integration of the Bison Calf

The integration of the calves into the herd is the process by which the calves become true members of the society into which they are born. There are two important processes involved. One is the development of the calf so that its behavior, at first markedly different from that of the adults, comes instead to resemble adult behavior. The other is the gradual loosening of the close bond between the cow and her newborn calf, so that the calf becomes an independent member of the society. The two processes go together, and the calf becomes independent from its mother at the age of about nine months, when weaning is usually complete. From the data presented in this section I think it is possible to show how this social development of the calf takes place.

Bison calves are precocious at birth. They stand up and suckle within just a few minutes of birth, they can run within an hour of birth, and they join in play groups at five days. They show adult feeding behavior, -- grazing and drinking water— when only two or three days old, and very soon other adult behavior patterns appear in the calf. Mounting behavior was first seen in two calves aged 6 and 14 days, and the lip-curl posture in a calf 10 days old. Although some actions are uncoordinated at first, or differ in some way from the adult behavior, this state soon changes, and these actions appear the same as they do in adults. This rapid

development means that in a very short time, the calf's behavior closely resembles that of adult bison. By the time a calf is three to four months old, its behavior is the same as in yearlings, except that it still suckles, and plays with other calves.

Not only do the individual behavior patterns come to resemble those seen in adult bison, but the calf's rhythm of activity is soon the same as that of adults. As already mentioned, when calves first start grazing, they only do so for a short part of the time that the older animals spend grazing, but gradually they spend longer and longer periods grazing, and only lie when the rest of the herd is resting. In addition, calves drink at the same time as the rest of the herd does, and most play between calves takes place in the evening, which is the time of greatest activity in the herd. Suckling becomes reduced from the frequent, irregular suckling of the first two days of the calf's life, to occurring three or four times a day, usually as the herd moves off to feed after a resting period. This results in a minimum of disturbance in the rhythm of activity of the cow and calf.

At first a close bond exists between a cow and her calf. This is shown in the way the cow prevents all contact between her calf and other herd members, and in the way the calf always runs back to its mother while exploring, playing, or after any new or frightening experience. Probably it is during the first few hours of the calf's life, when it is alone with its mother, and through the frequent physical contacts

with its mother during the calf's first few days, that this bond is formed. This bond is slowly loosened, and it appears that the calf takes the initiative in this. The calf begins to make social contacts with members of the herd other than its mother. The first such contacts tolerated by the cow are the brief ones that the calf makes as it explores around her. At the same time the cow stops grazing between her calf and the rest of the herd, and when the calf is about five days old, the cow stops preventing more prolonged contacts between her calf and other animals, and the calf begins to play with other calves. From this time on, interactions between calves become more frequent, occurring at any time that the herd is active and not resting, and involving play-fighting and mounting behavior as well as chasing.

As suckling in the calf becomes restricted to a few times each day, contacts between a calf and its mother become less frequent. Suckling periods also get shorter as the calf grows older. Two- to four-week-old calves suckled up to 12 minutes at a time, while four-month-old calves did not suckle for more than six minutes. This means that the calf not only comes into less frequent contact with its mother after its first few days of life, but also that these contacts become shorter when they do occur.

I have already briefly mentioned the cow-calf subgroup. At first the cows are responsible for its existence, because they graze and lie down close together, and the calves

follow their mothers. This sub-group increases the likelihood that a calf's first social contacts and probably also its later ones with animals other than its mother are with other calves. This is interesting because yearlings and two-year-olds also interact more often with members of their own than other age groups. Later the calves themselves are responsible for the existence of a calf sub-group because they come to prefer the company of one another to that of their mothers. Thus the behavior of the cows helps to begin a pattern of behavior in the calves which persists in subadults.

I have discussed in more detail in the section on the rut, the aggression that cows occasionally show towards their calves during the rut. This occurs when a bull is paying attention to a cow. She sometimes makes an aggressive head-jerking motion towards the calf, which then moves out of the way of the cow and bull. Probably this behavior of the cow is a factor in the loosening of the bond between cow and calf.

It seems, then, that there are several factors important in the integration of the calf into the social structure of the group, -- the precociousness of the calf at birth, the rapid development of its behavior and the formation of a rhythm in its activities, the making of social contacts with different members of the herd, and the gradual loosening of the bond between the calf and its mother. Probably the most important of all these is the calf sub-group. This helps to increase

the independence of a calf from its mother because of the preference the calf comes to show for the company of other calves. Thus in the company of the rest of its age group, each calf becomes a member of the society, as its behavior comes to resemble more and more that of the other members of the herd.

THE RUT IN BISON

Introduction

Although the main subject of this work is the behavior of calves, I decided to try to obtain some information on the rut in bison. The historical literature is contradictory in many respects. The most complete works on the behavior of bison during the rut are those of McHugh (1958) and Fuller (1960). Questions still unsolved concern what proportion of the bulls take part in the rut, what role is played by the numberous lone bulls seen during the rut, and whether or not the two- and three-year-old bulls leave any progeny under natural conditions.

Preliminary observations on rutting behavior were made in Waterton Lakes National Park. It was hoped that information on the rut could be obtained from observation of this herd, the members of which could all be individually recognized by the time of the onset of the rut. However, when by the middle of August, very little rutting activity had been seen in that herd, it was decided to continue observations in Wood Buffalo Park. I left Waterton on 15 August and from 21 August to 15 September 1961, observations were all made on the wild herds in Wood Buffalo Park. I stayed at the Buffalo Management Camp at Sweetgrass, near Lake Claire, and observations were made on the herds of bison within a three-mile radius of the camp. By working in Wood Buffalo Park I was also able to compare the behavior of the

small confined herd in Waterton Park with that of the wild bison in Wood Buffalo Park.

The Rutting Season

It has been noted by various authors that the rutting season in bison occurs in July and August. Fuller (1962) states that in Wood Buffalo Park mating activity begins in July and that the peak is reached between 10 and 20 August. McHugh (1958) found that in the Hayden Valley herd in Yellowstone Park, mating activity extended from 15 June to 30 September with most of the rutting occuring between the end of June and the middle of September, and that in the Wind Cave herd in South Dakota the rut ran from about 23 June to 14 September. These dates seem to indicate that the rut begins earlier in the bison in Wyoming and South Dakota than it does in the northern bison in Wood Buffalo Park, so that calves should be born earlier in the south than farther north. According to K. F. Cooper (pers. comm.) almost all births in Wood Buffalo Park occur in May, with a very few in April and some in June. McHugh (1958) reported that in the Lamar Valley herd in Yellowstone Park calving began in mid-April and ran till the end of May, with most of the calves being born in the first half of May and only a very few in June. Bad weather is common in the north in April and would probably lower the chances of survival of a calf born at that time. If these dates are consistent over a number of years then the later rut and calving season in

Wood Buffalo Park may be an adaptation ensuring that calves are born late enough to miss the bad weather.

The occasional birth of bison calves in months other than the normal calving season has been reported (McHugh 1958). In Elk Island Park a calf was born in the corral at the time of the roundup in November, 1961, and the same thing occurred in Wood Buffalo Park in 1960. K. F. Cooper told me that in Wood Buffalo Park he has seen occasional new born calves in every month except February. This shows that cows occasionally come into estrus at times of the year other than the rutting season. During the rutting season, cows are probably polyestrous, with a cycle of about three weeks, according to Fuller (1962). These observations also suggest that at all times of the year at least some bulls are fertile.

The Herd Structure in Wood Buffalo Park

During the time I was in Wood Buffalo Park, most of the bison were in small herds of 20 to 30 animals of various ages and both sexes. These herds will be referred to as "mixed herds". A few mixed herds of much larger size were also seen. The number of animals in these larger groups was usually about 50, 75, or 100 -- multiples of the number in the more common, small herds. I frequently saw these larger herds split up into smaller groups of up to 30 animals, which then moved off in different directions, and I also saw two or three small herds join to form one big one. This led me to believe that the larger herds were aggregations of the

smaller ones and that these large groups were far less stable than the small ones. I think the basic herd unit during the rut is a group of between 11 and 30 animals. These observations on grouping during the rut support those of Fuller (1960) and K. F. Cooper (pers. comm.) for former years and different areas of Wood Buffalo Park. They do not agree with the observations of McHugh, however, who found that group size in the Hayden Valley bison in Yellowstone Park was much larger during the rut.

Fig. 14 shows the number of animals in each of 48 mixed herds, counted in meadow habitat during August and September 1961. The average number per herd was 24.5. Table VIII shows the average composition of 35 mixed herds seen in the Lake Claire Area of Wood Buffalo Park, and that of the Waterton Park herd at the time of the rut. The figures for Wood Buffalo Park and the data in Fig. 15 are based on 35 of the 48 mixed herds shown in Fig. 14. It was impossible to determine accurately the composition of the remaining 13 herds, because these herds were either too large or were too far away. The size of the 35 herds ranged from 10 to 52 animals, with an average of 23.4, while the average of all 48 was 24.5. The difference between these two averages is due to the difficulty of classifying the individuals in large herds into age and sex classes and so the herds that were classified tended to be the smaller ones.

In six of the 35 herds classified there were a few

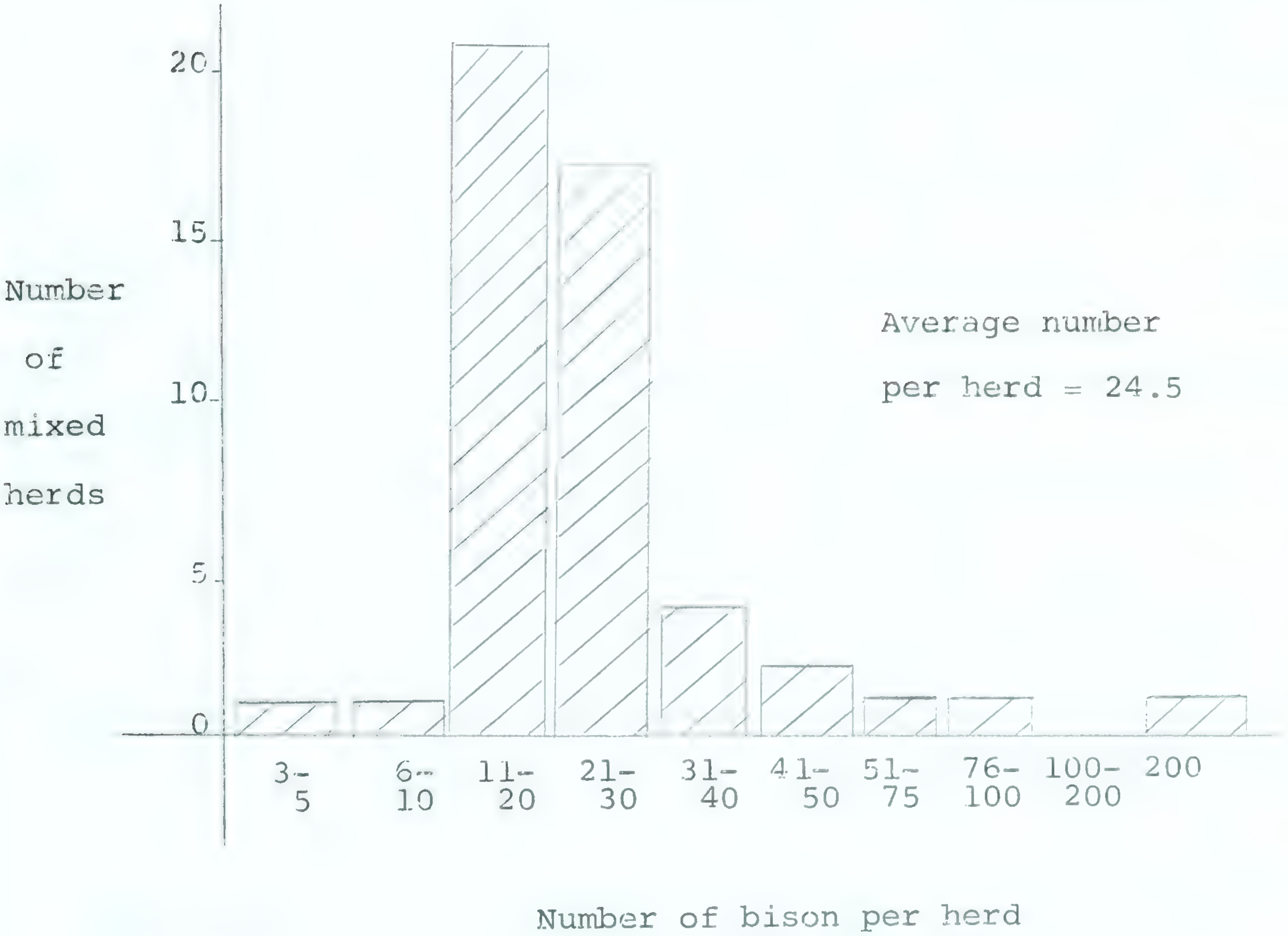


Fig. 14. Size of 48 mixed herds counted in meadow habitat during August and September 1961, in Wood Buffalo Park.

Table VIII. Composition of the Waterton Park Herd in August 1961, and average composition of 35 mixed herds, counted in meadow habitat during August and September 1961, in Wood Buffalo Park.

Age and sex class	Wood Buffalo Park		Waterton Lakes Park
	Total bison seen	Average* per herd	Number in herd
Adult bulls	103	2.9	4
Cows incl. two- & three-year-olds	395	11.3	13
Sub-adult bulls spike-horns	109	3.1	5
Yearlings	104	3.0	2
Calves	74	2.1	7
Unclassified	35	1.0	-
Total	820	23.4	31

* The figures for average herd composition in Wood Buffalo Park were obtained by dividing the total figures by 35.

individuals whose age and sex were not determined. The classes most difficult to distinguish were cows and two- to three-year-old bulls, so the unclassified animals probably belonged to one or other of these two categories. Only under exceptionally good observational conditions was it possible to distinguish two- and three-year-old cows from older ones. For this reason, although the two- and three-year age-group is treated separately for bulls, it is omitted for cows, and the figures for cows include all animals two years of age and up.

Table VIII shows that the composition of the Waterton Park herd was similar to the average herd in Wood Buffalo Park. The only discrepancy was in the number of calves of the year. Whereas there was an exceptionally poor calf crop in Wood Buffalo Park in 1961 and the average number of calves per herd in August and September was two (i.e. two calves for every eight or nine cows of breeding age), the Waterton herd contained seven calves by the end of July. This similarity in population structure between the Waterton herd and the wild ones suggests that at least during the rutting season, the Waterton herd was typical of the wild herds in its compositon. This was fortunate because it meant that no unnatural social behavior in the Waterton herd was caused by atypical population structure.

Fig. 15 shows the number of adult bulls in each of the 35 mixed herds. An important fact shown is that there

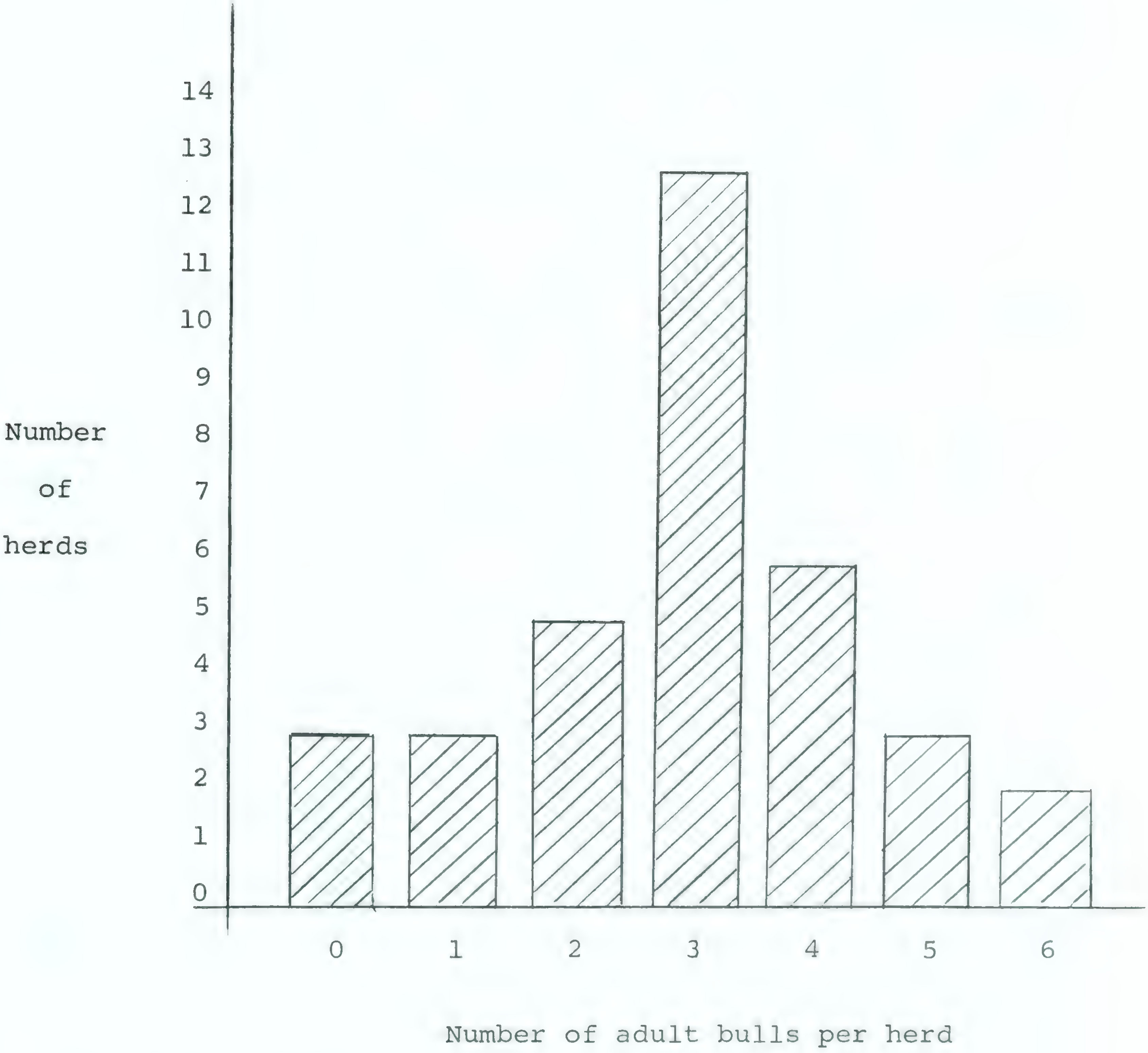


Fig. 15. Number of adult bulls in 35 mixed herds seen in meadow habitat in Wood Buffalo Park, August - September 1961

was almost always more than one adult bull in each mixed herd during the rutting season. The number of adult bulls in these herds ranged from zero to six, with an average of 2.9, a standard deviation of 1.53 and a distinct mode at three.

In addition to the small herd units seen in Wood Buffalo Park, there were large numbers of adult and aged bulls which were usually seen alone, but sometimes in pairs or small numbers together. I seldom saw less than 30 of these lone bulls each day, within a one-mile radius of camp. McHugh (1958) referred to the bulls which he saw alone or in small numbers together during the rut in Yellowstone Park as "bull groups". The words "group" and "herd" as used when speaking of ungulates usually imply a degree of cohesiveness and social structure which I do not think exists among the northern bison bulls during the rut. Observation of these bulls showed that even when there were as many as six of them within a few hundred feet of each other, they very seldom interacted with one another, and did not behave as the animals in a herd do. They would eat, drink, ruminate and lie down at different times, not together, as the members of a mixed herd do. For these reasons I shall refer to these animals as "lone bulls", although this does not always mean they were alone, i.e. out of sight of other bison. This solitary behavior of the bison bulls during the rutting season is very different from that seen in the spring and early summer, when herds of up to 40 bulls may be seen

(Cooper, pers. comm. and my own observations 1962). In these groups the bulls do show some coordination in their behavior. They move around together, and graze and lie down at the same time. However, as McHugh also found, the coordination of these bull groups is far less than that within a mixed herd.

RUTTING BEHAVIOR

The Occurrence of Rutting Behavior

McHugh (1958) stated that rutting behavior in Yellowstone Park was most intense in the early morning and late afternoon. I would not agree entirely with this for the northern bison because in certain circumstances (see below) rutting activity appeared to be as intense in the middle part of the day as in the morning or evening.

Rutting behavior was controlled by two main factors: the general mood of the herd (i.e. whether it was active or resting) and the weather. Rutting did not occur when most of the herd was resting. It occurred during grazing periods and especially when the herd moved off to feed after a period of rest. Schloeth (1958b) found the same thing in the Camargue cattle. Rutting never occurred during rain. I never saw a bull even sniff a cow during rain. It seldom occurred during hot, sunny weather or when there was a strong wind, even if the herds were moving around. Darling (1937) found that weather strongly affects rutting activity in red deer, *Cervus elaphus*. He found that cold dry weather stimulated sexual

activity and that activity remained intense if the weather became warmer, as long as it remained dry. Activity was far lower in humid weather. In bison, rutting activity was greatest in cool weather, whether dry or damp, and least during very hot weather and rain. Intense rutting activity was seen at any time of day provided the weather was right. The lowered temperature in the evening meant that intense rutting activity was frequently to be seen at that time. As already pointed out, it is at this time that the general activity of the herds is greatest, and play between calves and play-fighting between young bulls most often takes place.

Characteristics of the Rut in Waterton Lakes National Park

The onset of the rutting season in bison is characterised by an increase in restlessness on the part of the bulls, (Fuller 1960), including wallowing, bellowing and fighting (McHugh 1958). Very little increase in restlessness and no fighting at all were seen in the Waterton herd although constant observations were maintained. The significance of this lack of the type of behavior normally associated with the rut was only realized later, when I was working on the wild bison in Wood Buffalo Park. This will be discussed later.

One change which was observed in the Waterton herd as the rutting season approached was an increase in the frequency of investigation of cows by bulls. This included sniffing and licking of the vulva of the cow, "tending" of

cows, and attempts at copulation.

Another change occurred in the Waterton Park herd shortly before the rutting season. This was the breaking up of the bull group which was mentioned earlier. During July the five bulls in this group were less and less frequently seen together. Instead, the two most dominant bulls were often seen grazing or lying away from the rest of the herd. At first they were usually near one another, but during August they would wander alone, away from each other and from the herd. At intervals they would return to the herd, sometimes together and sometimes separately and investigate the cows by sniffing them. The significance of this behavior, and of the "tending bond" is discussed in the next section.

Rutting Behavior in Wood Buffalo Park

Behavior of the Wood Buffalo Park bison during the rut appeared to me to fall clearly into two categories, that occurring within the mixed herd unit and that occurring between mixed herds, or between mixed herds and lone bulls. I shall therefore discuss this behavior under the headings of "intra-" and "inter- herd" behavior.

Intra-Herd Behavior

There was no difference that I could detect between the bison in the Waterton herd and the northern bison in their sexual behavior within the herd. In both groups it consisted essentially of olfactory investigation of cows by

bulls, the "tending bond" and attempts at copulation.

The Lip-Curl Posture

The sniffing of a cow by a bull was usually followed by the lip-curl posture described earlier (Fig. 16). McHugh (1958) stated that there were indications that this behavior was omitted when the cow showed no signs of heat, but I could detect no difference in behavior or appearance between the cows which induced the lip-curl and those which did not. McHugh found that urination on the part of the cow was a stimulus to bulls nearby to sniff the cow. This was also the case in the bison that I watched, but in addition it seemed that sniffing by the bull was sometimes a stimulus for the cow to urinate. Frequently a bull would approach a cow and sniff her genital region (Fig. 17). She would then urinate. He would then wet his nose in the falling urine and then display the lip-curl posture. This behavior was also seen in bison involved in a tending bond. Frequent urination is characteristic of female horses in estrus, even when the only male nearby is a castrate, and in this species it appears to attract the attention of the male in the same way as it does in bison (my own observation). In dogs, (Beach and Gilmore 1949) and probably in many other carnivores, frequent urination by the female in estrus and the changed hormone content of her urine serve to advertise her presence and condition to males which may enter the female's home range. Presumably in bison the male can tell from sniffing the urine of

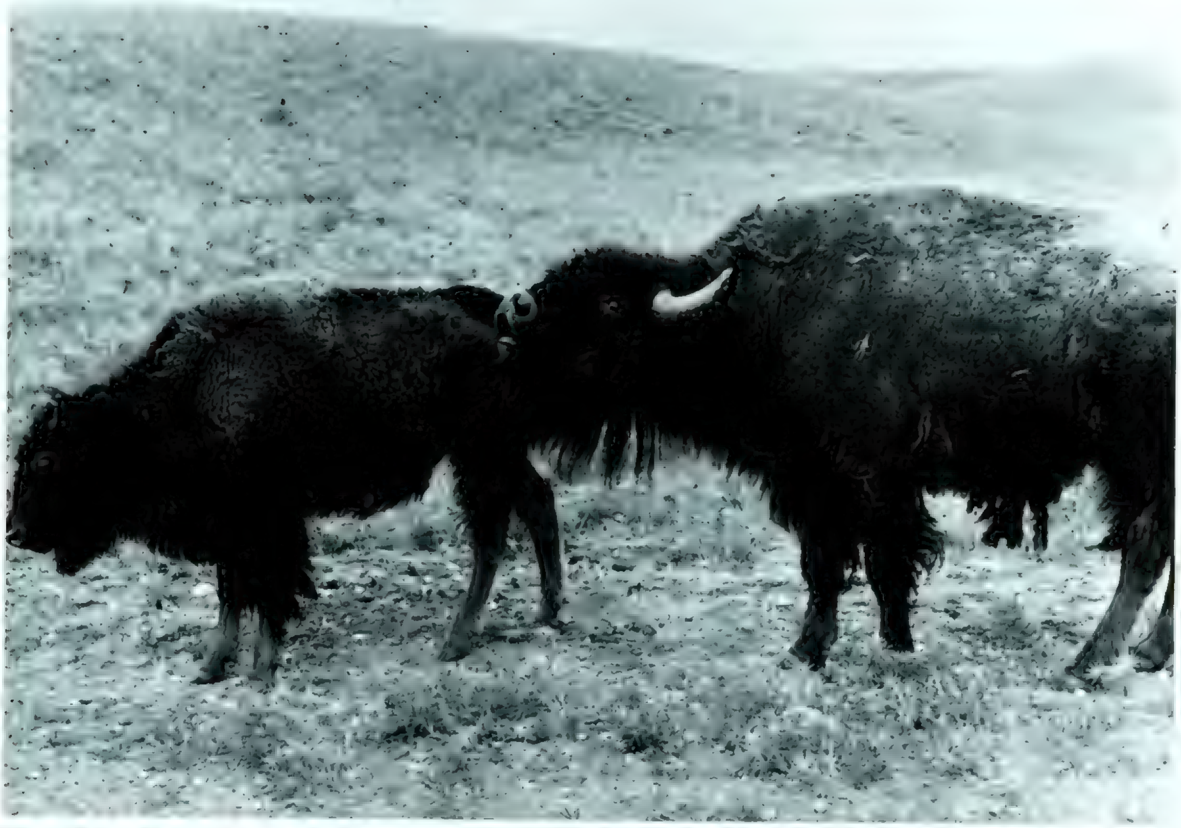


Fig. 16. The lip-curl posture, shown here by a two-year-old bull after sniffing a yearling bull.

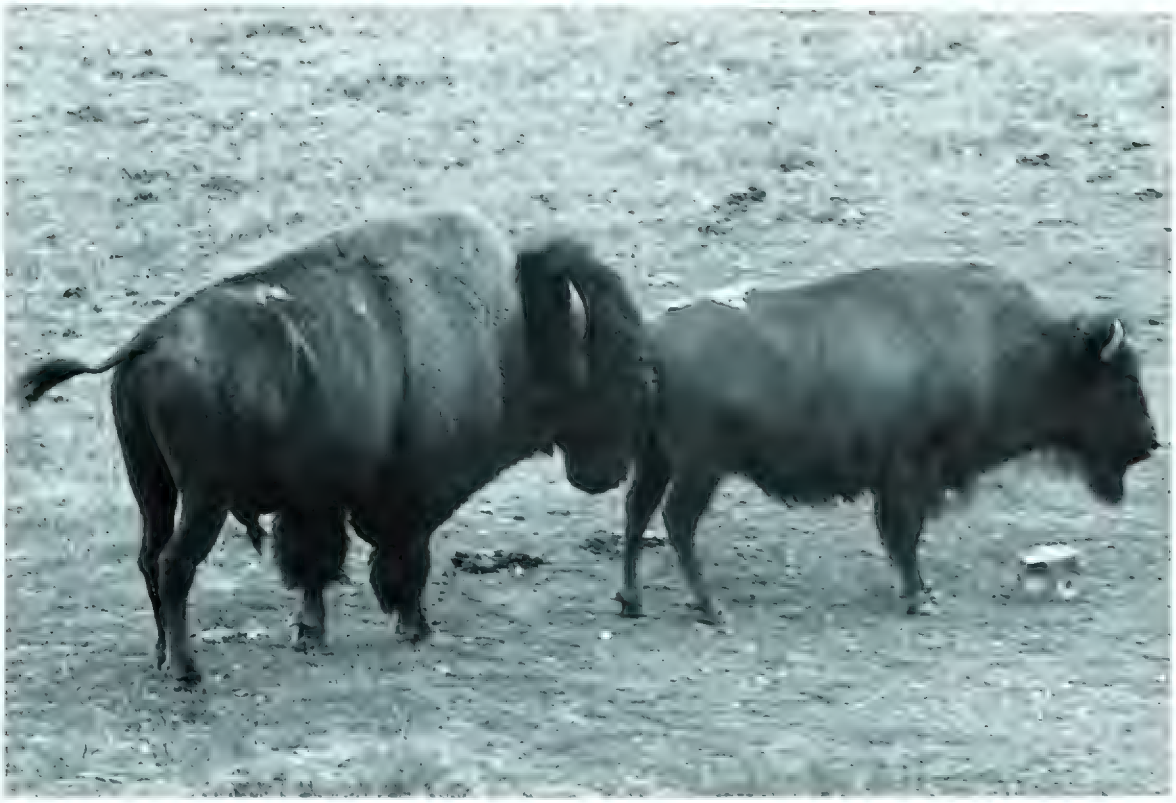


Fig. 17. A bull sniffing the genital region of a cow.

the female whether or not she is in heat.

The lip-curl posture, so often seen in bison, is known to occur in domestic cattle, though I could find only one published reference to it (Brownlee 1950). This behavior has also been seen in other bovids including the Camargue cattle, (Schloeth 1961), the "aurochs" raised by Heck (1954), and the yak, *Bos grunniens*, (my own observation, 1962). It also occurs in the moose, *Alces americana*, (Altmann 1959); the American elk, *Cervus canadensis*, (Altmann 1952); the red deer, (Heck 1956); the chamois, *Rupicapra rupicapra*, (Knaus 1960); the giraffe, (Innis 1958), and the domestic horse, (Von Raesfeld 1957). Probably, as more work is done on the behavior of ungulate species, this behavior will be found to be even more widespread. I think it likely that it occurs in all bovids. I found as McHugh (1958) did, that in bison the lip-curl posture was displayed after sniffing of a wide variety of objects, not only after sniffing a cow. Such objects included blood from an injured bison, mucus from a newborn calf (on the ground and on the calf itself), the placental membranes hanging from a cow before and after calving, and a clump of bison hair on the ground. Thus, it is not associated solely with sexual behavior, although in my experience it was most often seen in this connection.
Perhaps the explanation of this behavior is that it improves in some way the sense of smell of the animal. Probably its normal function (despite Brownlee's reference to it

as the "disgust behavior pattern") is as Innis (1958) suggested -- it is a means by which the male tests the urine of the female, as the hormone composition of the urine changes with the estrus cycle. By this means the male can tell if the female is coming into heat.

The Tending Bond

McHugh (1958) has termed the close association between a bison cow and bull during the rut the "tending bond". For other mammals, notably primates, a similar close association has been called a "consort pair" (Carpenter, 1934). McHugh (1958) and Fuller (1960) have described the phenomenon in bison fairly fully, and so it will not be described in detail here. It is characterized by a bull remaining close to one cow for a length of time -- sometimes a few minutes or hours, sometimes several days. During this time he follows her, and sometimes directs her movements and attempts to copulate. Tending was often seen to end without copulation. This, I assume, was because the cow was not in estrus. When the cow is in estrus, copulation is presumably the climax of the tending bond, and soon afterwards tending ends.

Fuller (1960) and McHugh (1958) both noted that a tending pair usually takes up position near the edge of the herd. I found that this was often the case, but tending pairs also frequently occurred towards the center of a group. When a pair was at the periphery of the herd, the bull maneuvered constantly to keep the cow away from the herd. Some bulls

appeared to be far more active in this respect than others. It is not known whether this varied with the bull, or whether it depended upon the condition of estrus of the female.

A bull sometimes directed a cow's movements with a jerking head movement. In some cases this movement occurred every minute or two, and was sometimes accompanied by a raising of the tail, sometimes also by partial erection of the penis. This head jerk seemed to be an intention movement preceeding an attempt to mount. Following the head jerk, if the cow did not immediately walk forward, the bull often attempted to mount by levering his head onto the rump of the cow, at the same time rising slightly onto his hind legs. I saw many of these mounting attempts in bison but not complete copulation. As Garretson (1938) pointed out, copulation in wild bison is very rarely seen by the human observer. Garretson (1938) and Fuller (1960) have both suggested that this is because it occurs most often at night, and this may be true. McHugh (1958) gave no indication of the time of day of the six occasions on which he observed copulation in bison, but K. F. Cooper (pers. comm.) told me that on the two occasions he saw it, it was late in the afternoon. I think that the lack of observations is probably mainly because copulation in bison, as in domestic cattle, takes only a few seconds (McHugh 1958, K. F. Cooper pers. comm., and my own observations on domestic cattle). Also, in wild bison, it would only be observed in a herd that had been undisturbed

for some time, and for the casual observer this condition is seldom fulfilled.

Age of Tending Bulls

With two exceptions, only fully mature bulls were seen tending cows in the herds in Wood Buffalo Park. Younger bulls, probably four to five years old, and "spike-horns" (two- to three-year-olds) were occasionally seen investigating cows, but their attempts were always interrupted by more mature bulls, and the younger animals simply moved out of the way. There was never any fighting in these circumstances. It appeared that the younger bulls recognized the superiority of the older ones and there was no aggression apart from an occasional jerk of the head from the older bull.

There was definite evidence that the actions of the younger bulls in investigating cows and in displaying the lip-curl posture attracted the attention of the older bulls and in this way raised the intensity of rutting behavior in the herd. On several occasions in both Waterton and in Wood Buffalo Park, adult bulls, either grazing or standing ruminating, were seen to look at another bull investigating a cow, then walk towards the pair, and the younger animal would move off.

McHugh (1958) found that tending bonds involving young bulls only lasted a short time. One of the two-year-old bulls in the Waterton herd, however, tended a cow persistently for over a week. During this time the older bulls

took little or no notice of the pair, but later, four bulls higher in the dominance hierarchy than the two-year-old were seen tending this cow. Only one bull was involved at a time. The first was the lowest of the four in the hierarchy, the last was the highest. Where replacement of one bull by another in this series was seen, there was no fighting, only occasionally a slight, head-jerking threat by the higher ranking of the two bulls.

I doubt if there is any fixed dominance hierarchy in wild bison because I do not think the herd units are stable enough. McHugh (1958) gives evidence that a cow herd in Yellowstone Park gained new members as it wandered near another herd. I saw two cows which were so distinctively marked that I am certain I could recognize them, in different herds on the two occasions when I saw them. Bulls wander freely in and out of the mixed herds during the rut, and this means that they are probably not in the same herd for very long, so they would not have much chance to learn to recognize one another individually, as they probably did in the Waterton herd. However, I saw no fighting at all between bulls within a herd in the wild bison. I can only suppose that immature bulls simply recognized adult bulls as superior, and that when two bulls which seemed to be about equal in size and age were involved, one gave way to the other as a result of signals too subtle for me to notice.

Fuller (1962) has shown that probably all male

bison three years old and more are sexually mature, while about a third mature as two-year-olds, and a small proportion as yearlings. There are records of yearling and two-year-old bulls of both the American and European bison breeding in captivity, (McHugh 1958 and Mohr 1952). However, because of the way that the younger bulls were always interrupted by older ones if they showed any interest in cows, I think it is unlikely that any bull younger than five years of age actually breeds in the wild state.

Atypical Tending Bonds

I did not see any tending behavior involving calves, such as McHugh (1958) described. I saw abnormal tending behavior on only two occasions, both in Wood Buffalo Park. These were tending bonds involving, in each case, two cows. One of each pair behaved exactly as the bull does, sniffing the cows, showing the lip-curl posture and making mounting attempts preceeded by a head-jerking movement. In one case this behavior lasted ten minutes, in the other five minutes. de Alba and Asdell (1946) describe exactly similar behavior in domestic cows, and they state that this display of masculine behavior is characteristic of cows in estrus. I could not tell if the bison cows were in estrus. In one case there were no bulls present, but in the other, where there were bulls, they took no notice of the tending cows, which suggests that the cows were not in heat. On three other occasions, twice in Wood Buffalo Park and once in Waterton Park, a cow

was seen sniffing another cow and showing the lip-curl posture. In none of these cases did tending behavior follow.

Inter-herd Behavior

Any behavior involving interactions between herds, or between herds and lone bulls, is here classed as inter-herd behavior.

Interactions with Lone Bulls

It has already been mentioned that large numbers of lone adult bulls wander over the meadows in Wood Buffalo Park during the rut. Probably some of these bulls are aged and do not take part in the rut. The majority play an important role. Very often, lone bulls could be seen lying or grazing within a few hundred yards of a mixed herd, and they behaved in the same way as the two dominant bulls in the Waterton herd did during August. As a mixed herd moved along grazing, one or more of these lone bulls would approach the herd, and walk through it, sniffing the cows. Sometimes a cow was induced to stand up, either by a bull just standing over her, or by him making a head-jerking movement in the air. I never saw a bull actually prod a cow into standing. I found, as McHugh (1958) did, that during these checks, a bull would walk through the group and sniff each cow in its path.

Following entry into the herd and investigation of the cows, the bull would do one of three things: It would

either wander right through the herd, leave it and graze alone again; remain beside one of the cows it had investigated and tend this cow; or remain in the herd, grazing with the other members, but not tending a cow. On one occasion I saw a mixed herd grazing towards nine lone bulls. As the herd approached, seven of these entered it and grazed with the herd after investigating the cows. One hour later, only two of the seven were still in the herd, the rest having wandered off alone again.

Interactions with the herd members were not confined to rutting behavior with cows. Usually the entry of lone bulls into a herd was accompanied by the behavior which is generally associated with the rut: bellowing, pawing the ground, horning the ground and wallowing. This involved both the bull entering the herd and the bulls already in the herd, usually one of them to a greater extent than the others.

This behavior usually followed a fairly fixed pattern. As the lone bull approached the herd he would bellow. I prefer to call his sound a "roar". It sounds something like a lion roaring or a pig grunting and is quite unlike the bellow of a domestic bull. The roar would be answered by one or more bulls in the mixed herd. Often the bull approaching the herd stopped on the way, pawed the ground, horned it (Fig. 18) and wallowed, in that order. Sometimes a bull would leave the herd and perform the same behavior

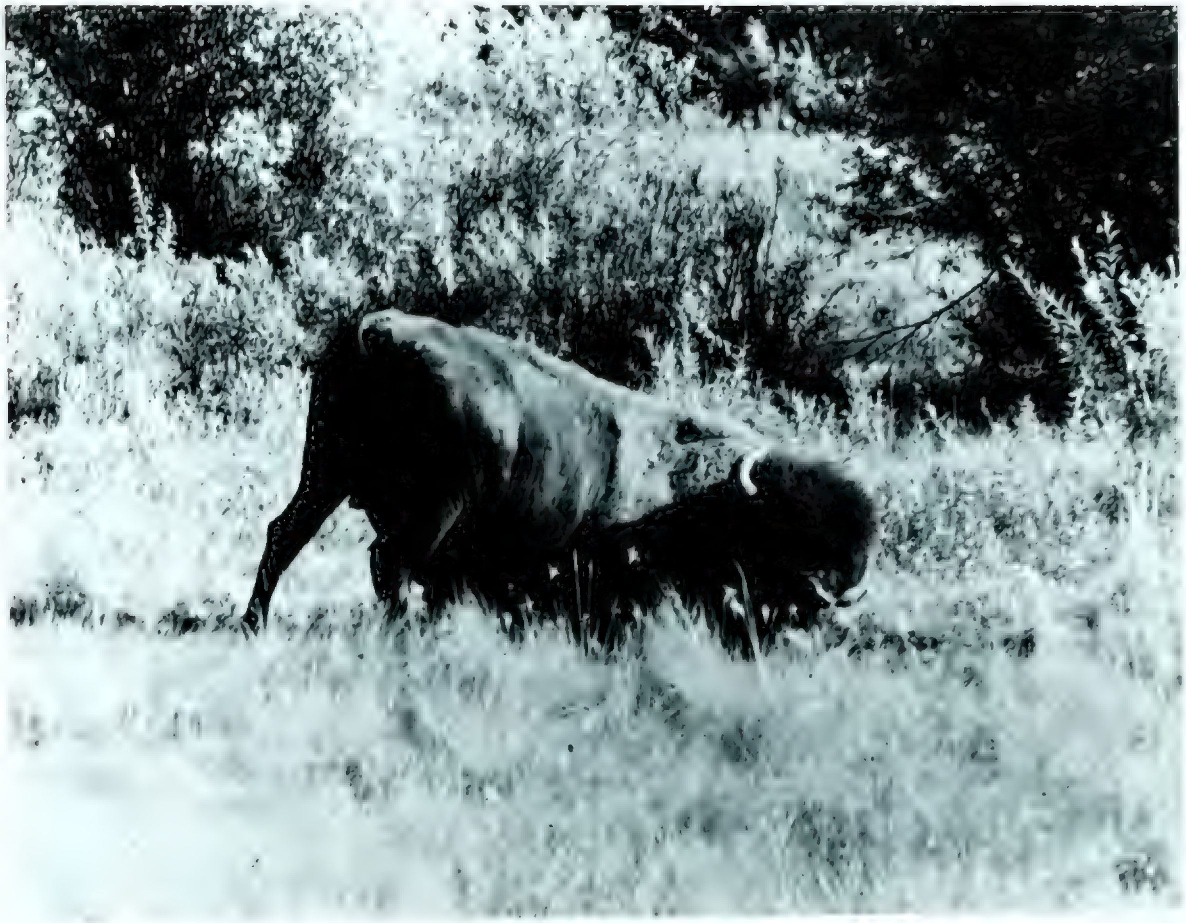


Fig. 18. A bull "horns" the ground.

while approaching the "entering" bull. On one occasion the entering bull stopped roaring and turned away from the herd after seeing this performance by the bull from the herd. On two other occasions, the two bulls reached one another, stopped, faced one another and the entering bull walked past the other, which then turned and followed it into the herd. An interesting point about one of these cases was that the entering bull was considerably smaller than the other, but was not deterred from entering the herd. I never saw fighting between a lone bull entering a group and a bull from the group, though I do not think my observations are extensive enough to say that fights do not occur in these circumstances.

The most significant aspect of this entry of lone bulls into mixed herds was that they always caused an increase in rutting activity in the herd. This was either direct, because bulls entering a herd almost always walked through it, checking the cows and often remained in it, tending a cow; or indirect because their entry usually resulted in a general disturbance and the bulls already in the herd would begin to investigate the cows. Often the bull which had left the herd to meet the entering bull would follow the strange bull through the herd, sniffing the same cows that it did.

Interactions between Herds

Considering the large number of mixed herds that were in the area near Lake Claire during August and September 1961, one would think that meetings between them would be fairly frequent. However, in three weeks of observations, I saw only six such encounters.

One of these cases involved two small mixed herds containing no adult bulls. The two herds met and intermingled with no interactions between members. The other five cases, involving herds which all contained more than one adult bull, were marked by numerous interactions between the bulls, and by varying degrees of disturbance. Since all five cases were different from one another I shall describe them, essentially as they were described in my field notes*:

> "August 22, 1961
>
> A mixed herd with 12 members approached a herd of 27 which was grazing. Each contained three adult bulls. As the smaller herd (Herd 2) drew near the larger (Herd 1) a bull (Bull 2) left it and walked

---

* I shall refer to the two herds of an interacting pair as Herd 1 and Herd 2 and to the bulls from these herds as Bull 1 and Bull 2. Different herds were involved on each occasion described.

slowly into Herd 1 erecting his tail as he approached. He and the most active bull in Herd 1 (Bull 1) then walked round Herd 1, with tails erect, sniffing cows. Then Bull 1 left his herd and walked in to Herd 2, also erecting his tail as he approached, and walked through Herd 2 sniffing cows. Meanwhile, Bull 2 stood in Herd 1 roaring. Bull 1 then walked to him slowly, also roaring and they walked stiffly round one another with tails erect. There was no fighting. Bull 1 then left Bull 2 in Herd 1, and walked, tail still erect, towards 2 bulls in Herd 2. One walked away and wallowed. The other stood roaring. Bull 1 and this latter animal then stood facing one another with their heads overlapping. (Fig. 20) Bull 1 then left and sniffed cows and then returned to his herd (Herd 1) and began to graze. Two of the bulls from Herd 2 wandered off alone grazing. Everything now quietened down, the two herds joined and all the animals began to graze.

August 23, 1961.

A mixed herd of 30, (Herd 1) including five adult bulls, was grazing. One of the bulls was tending a cow and roaring intermittently. Soon, answering roaring was heard and a mixed herd of 15 appeared. A bull in it (Bull 2) which was also tending a cow, and the bull from the larger herd (Bull 1) roared back and

forth, answering each other. A loud roar from the bull of one herd caused a louder roar from the other. The two herds met and coalesced with no commotion. Bull 2 walked through Herd 1 but did not go near Bull 1. The members of both herds grazed quietly.

August 29, 1961.

A herd of about 40 animals (Herd 1) was grazing and a smaller group (Herd 2) was lying a few hundred yards away. The animals in the latter herd got up as I approached and a bull (Bull 2) left the herd snorting and walked towards Herd 1. He roared several times and stopped to horn the ground and wallow three times on the way. A large bull (Bull 1) left Herd 1 and walked fast, roaring, towards Bull 2, which stopped, stared and started to walk away. He then stopped and faced Bull 1 and they walked round one another staring at each other. Bull 2 then entered Herd 1 and Bull 1 walked away and wallowed. Herd 2 grazed towards Herd 1 and the two herds gradually coalesced with no further interactions.

Shortly following this, a third herd of 25 bison (Herd 3) appeared. A Bull (Bull 3) left this herd and walked towards Herds 1 + 2, roaring and stopping to wallow once. Bull 1 left Herd 1 + 2 and walked quickly to meet Bull 3. They met in Herd 1 + 2 and stood with tails erect facing one another with their heads over-

lapping. Suddenly Bull 1 put his head down and they began to fight. The fight consisted of a series of vicious shoving matches each lasting about 30 seconds. Between bouts they stood with heads down, roaring, and appeared to put their horns in position again, one set above the other. Their tails were only erect when actually fighting. They lost ground alternately, each having a backward run of about 50 yards. The area covered was large. Some of the cows in the herds stood and watched. Four adult bulls approached the fighting pair, roaring, and walked stiffly around with tails erect. The fight, which lasted altogether about five minutes, ended abruptly. At the end of one of the bouts of fighting the combatants did not put their heads down, but stood with their heads raised higher than normal. Bull 3 turned towards Bull 1 which jerked its head at him and Bull 3 turned away. There did not seem to be a decisive winner, though Bull 3 backed a little more and turned away from Bull 1 at the end. In the 15 minutes following this, the disturbance died down, the three herds coalesced and all the bison began to graze.

September 14, 1961.

A herd of 23 including three adult bulls (Herd 1) was grazing along and began to draw near to a herd of about 80 (Herd 2) which was scattered in groups of about 20. As they got nearer, a bull (Bull 2) left

> Herd 2, and walking fast with tail down, it approached Herd 1. A bull in Herd 1 (Bull 1) started to walk towards Bull 2, stopping to paw the ground, horn it and wallow on the way. They met and stood facing one another with heads overlapping for 15 to 30 seconds. Then suddenly they began to fight. Again the fight consisted of several skirmishes each about 30 seconds long. Between bouts they stood with heads down, roaring. Three other adult bulls approached the fighting pair with tails erect, and walked slowly around, watching. The bulls crashed through the herd, covering a large area, and other bison moved out of their way. No calves were seen moving away. Again the fight ended abruptly with no indication of a winner or loser. For 20 minutes after the end of the fight, which lasted three minutes, adult bulls walked stiffly round one another with tails erect, but did not fight. The two which had fought walked away in different directions, not towards the herds from which they had come."

Different phases of fighting and the behavior preceeding it are shown in Figs. 19-23.

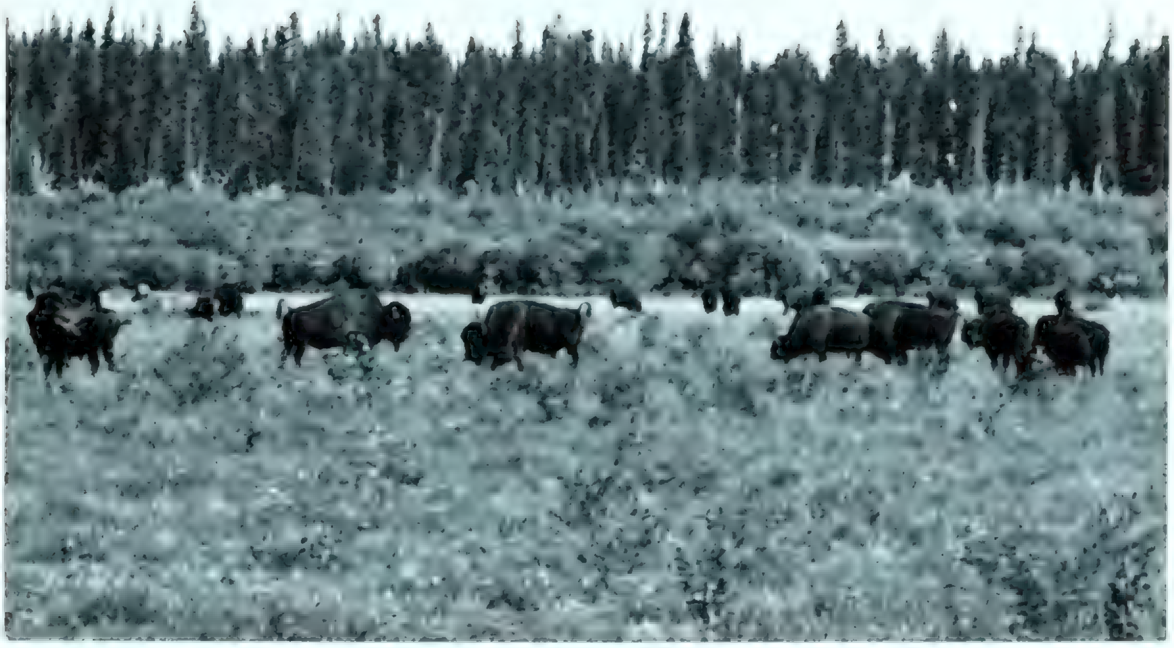
The Effect of the Rut on the Calves of the Year

Calves were affected by the rut in three ways. When a bull came to investigate a calf's mother, the disturbance of the cow and calf was often followed by the calf attempting to suckle. Further disturbance was caused if a calf was

suckling when a bull approached. This often resulted in the calf stopping suckling, running around to the other side of its mother, away from the bull, and trying to suckle again. A calf nearly always avoided bulls sniffing or tending its mother and stayed in such a position that the cow was between it and the bull.

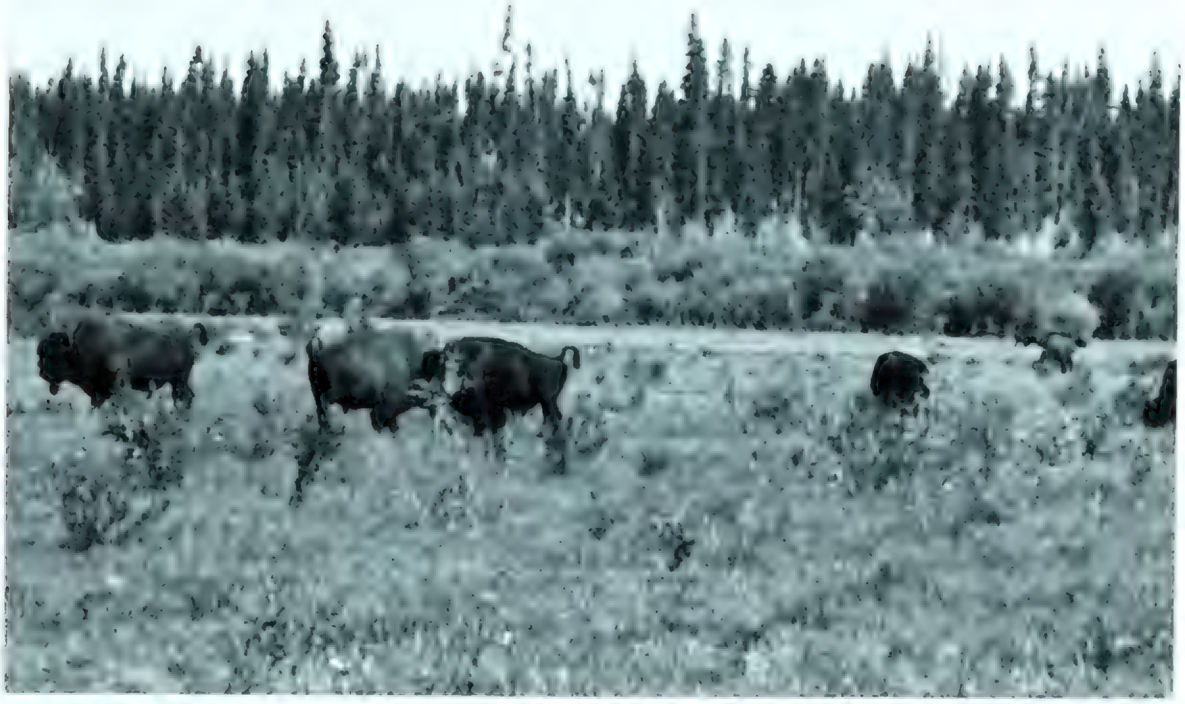
On several occasions cows being tended by bulls were seen to act aggressively towards their calves. These aggressive actions usually involved sideways head-jerking threats. The calf would move out of the way of the pair and usually grazed nearby. I think that this aggressive behavior, occurring as it does in July and August, when most of the calves are three or four months old and becoming increasingly independent, could be a significant factor in starting the weaning process, which is lengthy in bison and is not complete till the calves are about nine months old.

Before I began this study, I thoughtthat calves might be affected by the fighting between bulls which occurs during the rut. No fighting over cows was seen however, and while a few animals were seen to move out of the way of fighting bulls, there was never any danger of the calves being injured. Most of them are quite big by the rutting season and are quick on their feet, so that I do not think a calf would have any trouble getting out of the way if a fight should occur nearby.



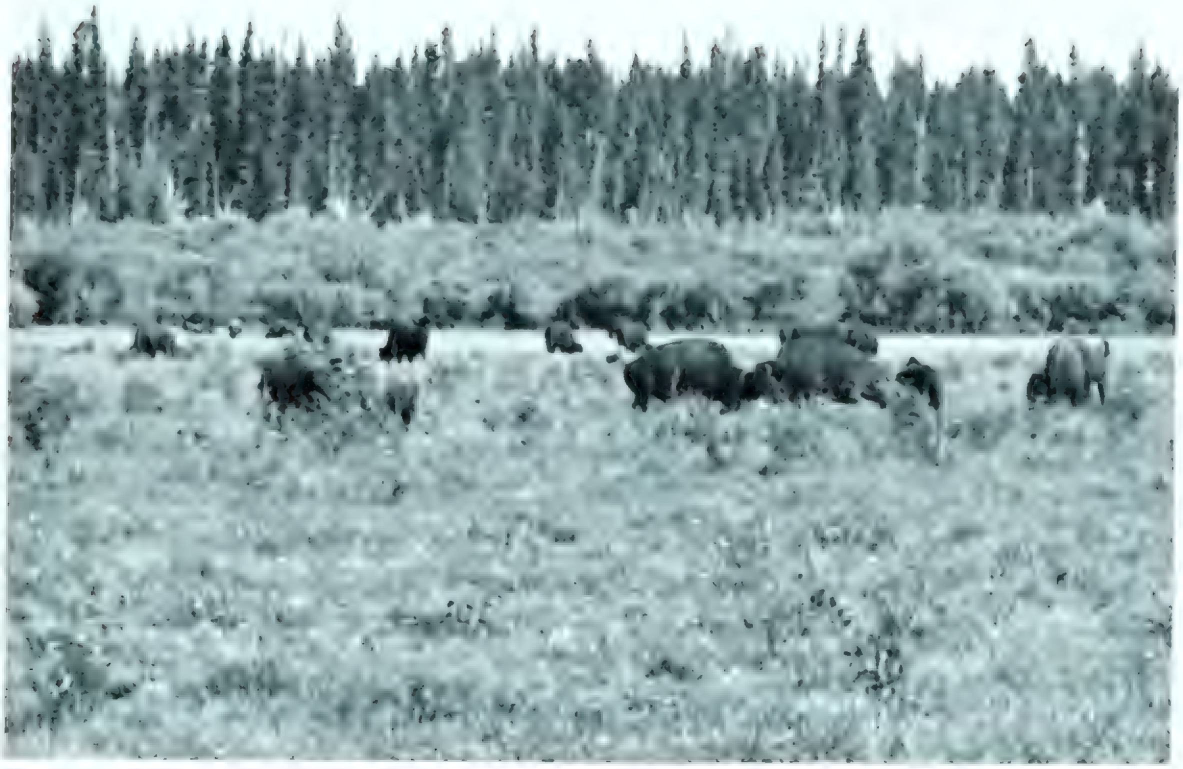
Fighting Behavior

Fig. 19. Two bulls from different herds approach one another, with tails erect.



Fighting Behavior (cont.)

Fig. 20. The two bulls stand opposite to one another with heads overlapping. Note the third bull standing nearby, with tail erect.



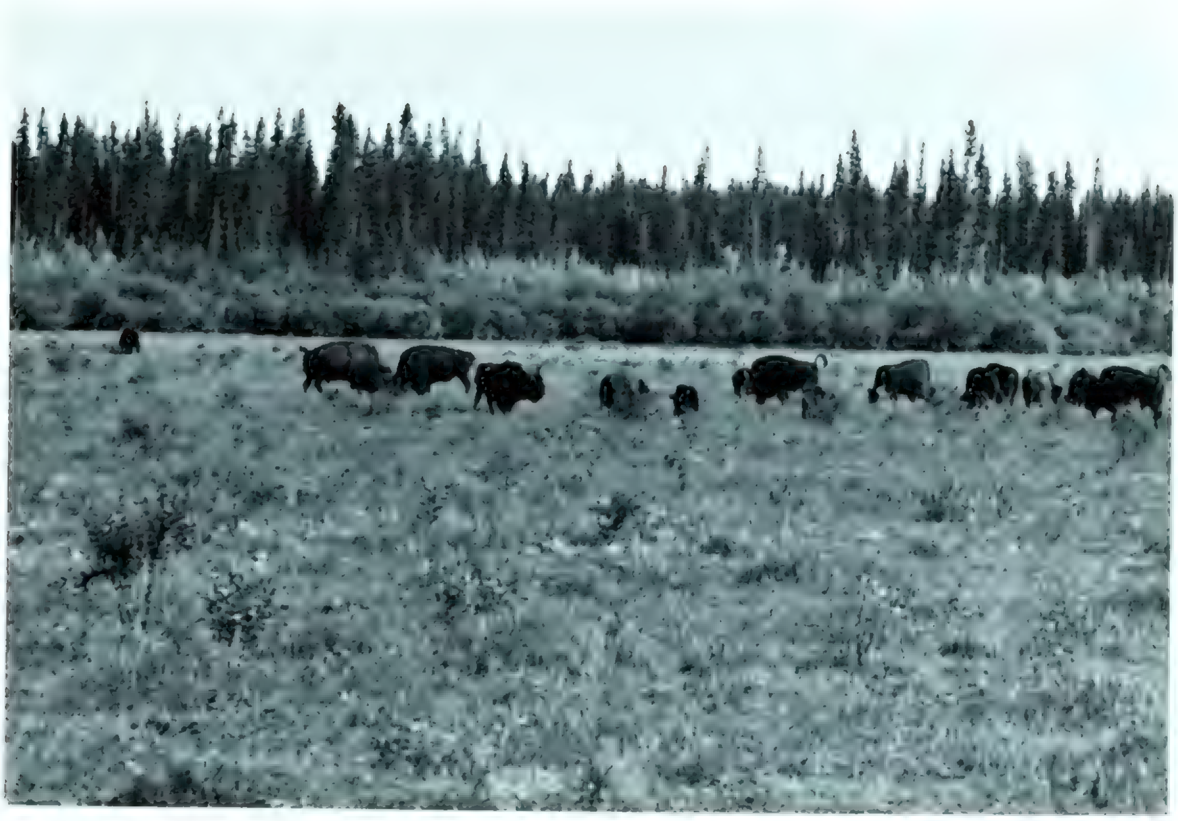
Fighting Behavior (cont.)

Fig. 21. The two bulls fight. The bull on the right is pushing the other one back.

[illegible]

[illegible]

[illegible]



Fighting Behavior (cont.)

Fig. 22. A pause in the fight. The two bulls stand with their heads together, and regain position for fighting. Note the two bulls approaching the combatants, with tails erect.

[illegible]

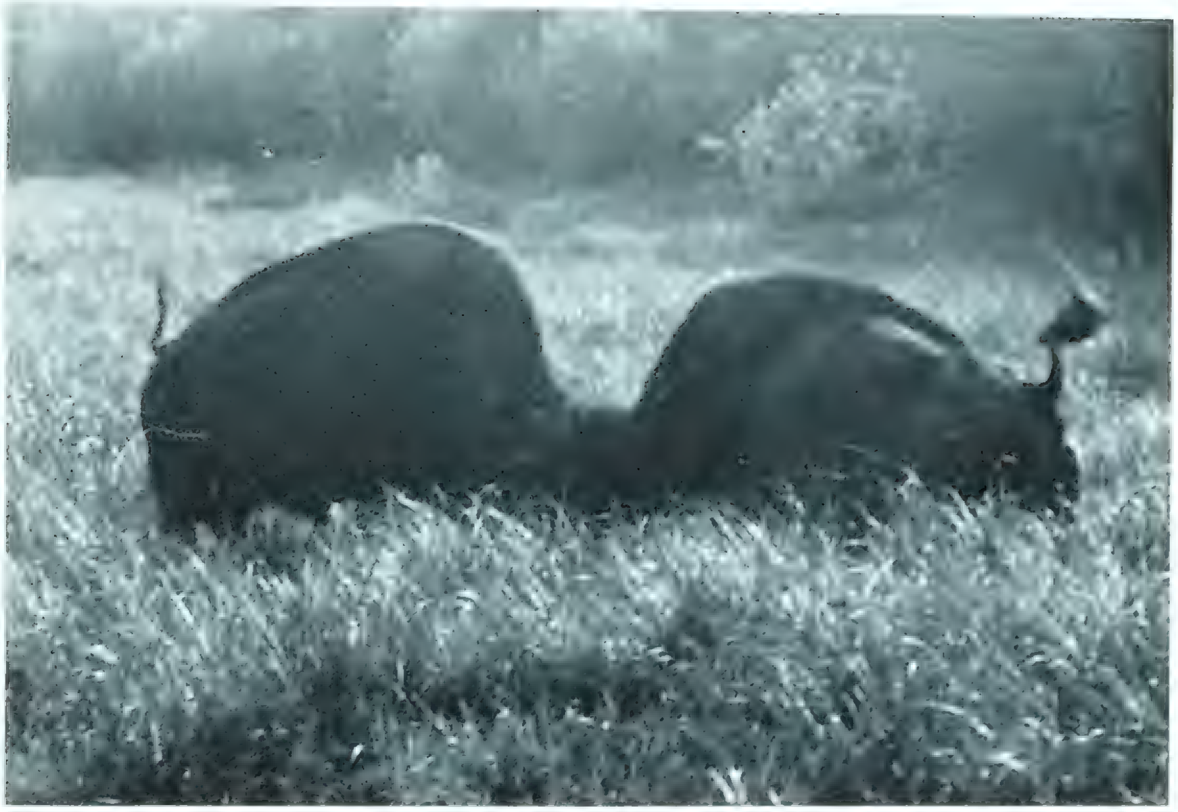


photo by K. F. Cooper

Fighting Behavior (cont.)

Fig. 23. Close-up of two bulls fighting. Note erect tails.

DISCUSSION

The Role of Different Bulls during the Rut

The questions of which bulls actually leave progeny and whether or not some breed more than others, are still largely unanswered. At present there is no information on the length of time any one bull stays in one mixed herd. There is nothing to show how long a given bull under observation in a herd has been in that herd. Apart from the indication that one bull was sometimes more active than the others in the herd, there is nothing to support the idea that one bull is "master of a harem", driving off other bulls and serving all the cows. As far as is known, a bull seen to be the most sexually active in a herd at one time may be behaving as a lone bull within the next few hours. The same could be true of the bull that leaves "his" herd, roaring, pawing the ground and wallowing as a strange bull approaches the herd. Supposing that the three or four adult bulls seen in a herd are permanently in it and that the lone bulls never stay long in a herd, there is still no evidence that the same bull within the herd is always the most active from one day to the next. The only way to answer these questions would be to follow a herd in the wild for several weeks -- a herd in which all the bulls could be distinguished and in which the bulls entering and leaving the herd could be told apart. In addition, observational conditions would have to be good enough and constant observation would have to be kept, so that

it could be determined which bull or bulls actually served the cows. To accomplish this, and to keep the herd as it is in the wild state, would be a difficult task.

Until these questions are answered, I think that the facts that there are almost always more than one adult bull in the herd and that there is constant movement of bulls into and out of the herds suggest that there is no regular master of the herd. The behavior of the two dominant bulls in the Waterton herd supports this suggestion. If in bison the normal situation was that one bull is master of each herd and serves all the cows, one might expect that he would stay in the herd all the time, if not actually tending a cow, then keeping away other bulls. The fact that both the most mature bulls in the Waterton herd spent little more than half the time with the herd during the rut, suggests that in the wild state also, no individual bull is permanently in the mixed herds and that probably all adult bulls spend some time as lone bulls. While some are more active than others, probably no one bull leaves very many more offspring than any other, at least not to the extent suggested by the idea that there is a master bull in each herd.

I think it certain, from facts given earlier, that bulls under about five years do not breed in the wild. It is also certain that these young bulls and the lone bulls play an important role in the rut, even if they do not actually

leave progeny, because they stimulate rutting behavior and increase its intensity. Without the presence of several bulls in a herd, I think that successful breeding would be reduced.

Fighting Behavior
and the Significance of Pawing, Horning, and Wallowing in Bulls

Apart from the context of grooming behavior, pawing the ground, horning it and wallowing were seen performed by bulls under the following circumstances:

1. when a lone bull approached a bull from a mixed herd
2. when two bulls from mixed herds were approaching one another
3. occasionally when two lone bulls came within sight of each other
4. when an adult bull left its herd and walked towards me
5. occasionally when a bull was tending a cow

McHugh (1958) lists similar observations. Sometimes, as McHugh also found, the pawing, horning and wallowing of one bull appeared to discourage another bull from coming any closer. Roaring appeared to act in the same way.

In view of the deterrent function of this behavior and the circumstances in which it occurs, it seems clear that roaring, pawing, horning the ground and wallowing are all part of a pattern of threat behavior. Probably these actions have become modified from grooming behavior to take on a new function, and roaring has evolved as a vocal threat which can be used at long distance. Erection of the tail seems to

be a sign of extreme readiness to fight. Garretson (1938) stated that roaring and pawing in bison are signs of an impending fight. Similar behavior in domestic cattle and the Camargue cattle has been described as threat by Fraser (1957) and Schloeth (1958b).

McHugh (1958) states that this behavior "functioned at times as threat" in bison, but says that in some circumstances, pawing and wallowing are "displacement activities". The circumstances he lists include pawing

1. by bulls during a pause in battle
2. by a cow in a corral when a human motioned towards her
3. by a cow with a newborn calf when approached by a human and when a larger bison cow investigated the calf
4. by bulls when approached by humans

These circumstances all appear to me to be ones in which one might expect threat behavior, and in my experience these actions were obviously being directed at another animal or a human, so I cannot see any justification for explaining pawing here as a displacement action.

It is important that although pawing and wallowing behavior were often seen, fighting was rare. Pawing and wallowing always preceeded a fight, but often it faded out as a bull joined a herd or two herds coalesced, and no fight followed. It seems then, that this behavior functions to prevent fighting.

I cannot explain satisfactorily why fighting occurs

in bison, since there does not appear to be any direct competition between bulls for cows. Following one of the two fights described, the two combatants went off alone and not to their respective herds, so it does not appear that the bulls were defending a "harem". The fighting and threat behavior accompanying encounters between mixed herds was always followed by a peaceful intermingling of the different herds. Perhaps a display of this sort is necessary before a peaceful coalescing of the herds is possible. On the other hand, in the case of lone bulls entering a herd, the display by the bull in the herd did appear to act as a deterrent to the lone bull in some cases, and he turned away from the herd. Hediger, (1949, cited in Bourliere, 1960), has described a form of territorial marking in European bison: the bulls mark trees with their urine by urinating on the ground, rolling in it, and then rubbing the trees. Perhaps the wallowing behavior of the American bison is a territorial display, the herd being a "mobile territory" and the bull displaying his "possession" of the herd by this pawing and wallowing behavior. However, if, as I think is the case, bulls do not stay very long in one herd, this explanation may seem rather illogical.

Possibly the explanation is this: that at any one time, one bull in a mixed herd is temporarily the most active one, and he shows this by means of the wallowing threat display when strange bulls or herds approach. As Schloeth (1958b) put it when explaining this behavior in the Camargue

cattle -- "L'animal affirme ainsi son statut social devant les membres de la société." (the animal asserts its social status in this way, before the members of the society). This display normally serves to demonstrate to the bulls, if not to the human observer, which one is superior, and thus, fighting is usually prevented. In a few cases threat behavior does not prevent fighting and a fight then occurs, not over a cow or cows or over ownership of a harem, but rather over temporary status in the herd. In this way, the most active and vigorous bulls would serve the most cows, with the minimum of fighting.

The Significance of the Tending Bond

There has been no discussion in the literature on bison concerning the significance of the tending bond. McHugh (1958) discussed the characteristics of the tending bond and mentions that he saw copulation occur. His account implies that he did not observe mating between the same pair that he had watched in the preliminary stages of tending. Since there is no published account, so far as I know, of anyone having watched a bison bull tend a cow, and observed the tending lead up to copulation in the same pair, it is perhaps easier to discuss the question with reference to domestic cattle, the behavior of which seems to be very similar to that of bison, in this respect.

Kerruish (1955) gives a description of the behavior which leads up to copulation in domestic cattle. Since, in

order to understand its significance, it is necessary to have a description of the whole process, I shall quote Kerruish's account:

> "Mating in cattle on free range is a prolonged process lasting sometimes as long as 60 hours. An experienced bull running with the herd, appears to be able to detect oestrus two or three days before its full onset. He will first single out the cow and for a day or two will keep very close to her, grazing and lying down within a few yards and keeping her under continual surveillance. As full oestrus approaches, the male exhibits increased interest and more intense excitement. This is sometimes shown by his licking and smelling the cow, especially around the vulva. Later, mounting is attempted but is met with repeated avoidance reactions, with consequent frustration of the bull's attempts at coitus. Finally as the climax of sexual excitement approaches and the female becomes receptive there may be partial erection and protrusion of the penis, dribbling of accessory fluid and repeated persistent attempts at mounting...."

This behavior seems to be exactly the same as that characteristic of the tending bond in bison. The excitement resulting from tending the cow is increased further by the threat displays which are performed if a strange bull enters the herd. I quote Kerruish's account further:

> "The intense sexual excitement described above is built

> up slowly to a climax. In the early stages the bull is little roused sexually, but by repeated stimulation through visual, olfactory and auditory receptors, a highly excitable nervous and physical condition is reached by the time coitus is achieved. It is probable that the excitement which accompanies precoital display has an effect not only on the sexual organs but also a general effect on body metabolism, on the level of secretion of the endocrine glands and on the vascular system, so that excitability and tone of the whole body are increased, and a more vigorous and better coordinated ejaculation is given at coitus."

This proposed explanation of the significance of tending behavior in cattle is supported, and an important aspect opened up by some experiments with bulls in Artificial Insemination Centers, described by Kerruish (1955). These experiments showed that bulls deprived of the sexual stimulation which results from their behavior under natural conditions, gave a poorly coordinated and less vigorous performance at copulation, with a consequently poorer sample of semen produced than did bulls which were stimulated sexually before semen collection. Results showed an 8.7 per cent higher conception rate in cows served with semen from bulls sexually stimulated before collection than in cows served with semen from the same bulls kept under conditions where they were not allowed the natural behavior before semen

collection.

I think the chief importance of the tending bond is the same as that suggested by Kerruish for domestic cattle. It is a form of courtship behavior. In a wild species, where the animals can wander over large distances, this behavior would have the added advantage of ensuring that a bull is near the cow when she becomes receptive.

I have mentioned how the behavior of immature bulls investigating cows and the arrival of strange adult bulls, with the consequent threat display, increase the intensity of rutting behavior in the mixed herds. In a situation where there was only one bull in a herd, and no lone bulls in the vicinity, I think it possible that breeding might be reduced because the one bull might not reach the right condition for successful breeding. This probably could not arise in the wild state, unless the species was nearing extinction in the area. Possibly it was a contributing factor in the final decline of the wild plains bison, after their numbers had been severely reduced by man.

Differences in Rutting Behavior between Bison in Waterton Park and in Wood Buffalo Park

It has been pointed out that no "threat-wallowing", roaring or fighting was seen during the rut in the Waterton herd, although this is behavior normally associated with the rut in bison. In this respect the Waterton bison differed from the wild ones. I subsequently found that the peak of

rutting behavior in Waterton cannot have occurred until September in 1961, because no calves were born in this herd in 1962 until June. This means that the peak of the rut in 1961 was after I left Waterton in August. It is possible that fighting behavior may have occurred during the peak of rutting in this herd, but I think it unlikely. The difference between the wild bison and the Waterton herd almost certainly lies in the fact that at Waterton there was only one herd. There was therefore no inter-herd behavior. Since fighting does not take place between bulls within a herd, but only between bulls of different herds, no fights occurred in the Waterton herd. In the intra-herd rutting behavior, on the other hand, and in other types of social behavior, there was no difference between the Waterton bison and the wild ones. The behavior of the Waterton herd was normal as far as it went, but was incomplete. Rutting behavior in bison can only be complete where there is more than one mixed herd in the same area. In such a situation, the inter-herd and intra-herd behavior are linked to form one process, and interact to result in successful reproduction of the species.

SUMMARY

1. Social behavior of American bison was studied in a confined herd in Waterton Lakes National Park and in wild herds in Wood Buffalo National Park. Chief objects of the study were to obtain information on calf behavior, the cow-calf relationship, and rutting behavior.
2. The main activities of bison, -- grazing, resting and ruminating-- occurred in a rhythm, alternating with one another, The effects of weather on general activity are described.
3. Certain behavior patterns not previously described in bison, are discussed.
4. Investigation of the social relationships among members of the Waterton herd revealed the existence of a linear dominance hierarchy. Threat behavior patterns recorded in the investigation, formed a series of increasing severity. Passive displacement reactions were important in revealing social relationships between herd members.
5. Interactions were more frequent, and aggression was stronger between animals adjacent in the hierarchy, than between those further removed. Bulls and cows with calves were involved in more interactions than were other herd members. Cows interacted frequently with young animals which showed interest in their calves.
6. Age and size were important in some cases in determining status.

7. The significance of a dominance hierarchy is discussed.
8. The calving season in bison is from April to June, with some variation between areas.
9. In some cases it was possible to distinguish pregnant cows by their appearance, several weeks before calving.
10. The behavior of cows before, during and after parturition, and behavior of newborn calves are described. The first contact of newborn calves with bison other than their mothers, occurs when the herd investigates the new calf. The success of a cow in preventing this investigation depends upon its rank in the hierarchy.
11. The first attempts of calves to suckle are described. Newborn ungulates probably have an innate tendency to search along a horizontal surface and in the corner between a horizontal and a vertical one. The exact position of the udder is probably learned.
12. The significance of cows staying away from the herd during and after parturition is probably that a bond is formed between cow and calf, while they are alone.
13. Play in calves involved running, bucking, chasing and fighting. In play-fighting, the winner was the older calf, except when the younger calf's mother was close by, or when a female lost to younger bull calves. In mounting, the mounter was the older calf, 73 per cent of the time. The significance of play is discussed.
14. Vocal communication between cow and calf is by grunting.

Cow and calf can recognize one another individually by this means.

15. Calf behavior differs from that of adults in standing up, lying down, wallowing, mounting and the lip-curl posture.
16. The average duration of suckling was 6.7 minutes. Calves usually stood parallel to the cow while suckling. Sometimes they suckled from behind the cow, and occasionally while the cow was lying down. Means by which calves stopped their mothers moving, or induced them to stand up, in order to suckle, are described.
17. Weaning is a gradual process. It is usually complete when the calf is between 9 and 12 months old, but yearlings occasionally suckle.
18. During the rut, the bison are in herds of average size 24.5, containing members of both sexes. There were, on the average, three adult bulls in each herd. There were also many lone bulls.
19. Weather, and the general activity of the herd, control the occurrence and intensity of rutting behavior.
20. Rutting behavior in the bison in Wood Buffalo Park, fell into two categories, inter- and intra-herd behavior. The former consisted of interactions between herds and between lone bulls and members of herds, and this differed from behavior in the Waterton herd. The latter consisted of sexual behavior, including the lip-curl posture and tending.

This was the same as in the Waterton herd.

21. The function of the lip-curl posture is not known. It may improve the sense of smell of the animal, and thus enable bulls to tell whether or not cows are in heat.
22. The behavior of animals involved in a tending bond is described. In wild herds, bulls less than five years old did not tend cows because they were interrupted by older bulls while investigating cows.
23. Fighting never occurred between bulls within a herd.
24. The actions of young bulls in investigating cows attracted the attention of older bulls, which then displaced the younger ones. Young animals appear to recognize the superiority of older ones, with no aggression occurring.
25. Although they are sexually mature by the age of three years, bulls less than five years old probably do not breed in the wild, because of interruption from older bulls.
26. Lone bulls play an important part in the rut. They enter and leave mixed herds freely, and increase the intensity of rutting behavior in the herds.
27. Entry of lone bulls into herds was accompanied by threat behavior, involving roaring, pawing, horning and wallowing from the lone bulls and those in the herds, but was not followed by fighting.
28. Fighting involved only bulls from different herds. It preceded intermingling of the herds, and was preceded by threat behavior, which sometimes appeared to prevent the

fight.

29. Fighting consisted of a series of brief, vicious skirmishes, during wich the combatants put their heads together and pushed. Bulls never charged one another. Fights ended suddenly with no obvious winner.

30. Calves were only affected by the rut when bulls investigated their mothers. Threat behavior, shown by cows towards their calves at this time, is probably important in starting the weaning process.

31. There is no evidence to support the idea that there is a master bull in each herd. Some bulls are more active than others, but it is not known if they remain so, from one day to the next.

32. The function of fighting is questionable, since it is not the result of direct competition for cows. It is probably over status in the herd, which is displayed by the threat behavior preceding the fight. In this way, the most vigorous and active bulls would serve the most cows, with the minimum of fighting.

33. The function of the tending bond is to act as courtship behavior, resulting in coordination of behavior of bull and cow.

34. Differences in rutting behavior between the Waterton bison and the wild herds resulted from the existence of only one herd in Waterton, with consequent lack of inter-herd behavior.

35. Rutting behavior is only complete when there are several herds in the same vicinity. Inter- and intra-herd behavior interact, under natural conditions, to form one process.

LITERATURE CITED

Adler, J., L. Linn, and A. U. Moore. 1958. "Pushing" in cattle: its relation to instinctive grasping in humans. Anim. Behav. 6 (1 and 2): 85-86.

Alba, J. de, and S. A. Asdell. 1946. Estrous behavior and hormones in the cow. J. of Comp. Psychol. 39 (2): 119-123.

Altmann, M. 1952. Social behavior of elk, Cervus canadensis nelsoni, in the Jackson Hole area of Wyoming. Behavior 4 (2): 116-144.

Altmann, M. 1956. Patterns of social behavior in big game. Trans. North Amer. Wildl. Conf., 21: 538-545.

Altmann, M. 1959. Group dynamics in Wyoming moose during the rutting season. J. Mammal. 40 (3): 420-424.

Bateson, G. 1955. At theory of play and fantasy. Psychiatric Research Reports 2: 39-51.

Bateson G. 1956. The message "this is play". p. 145-242. Group Processes. Trans. Second Conf. 1955 Josiah Macey Jr. Foundation. B. Schaffner. (ed.) New York.

Beach, F. A. 1945. Current concepts of play in animals. Amer. Nat. 79: 523-541.

Beach, F. A. and R. W. Gilmore. 1949. Response of male dogs to urine from females in heat. J. Mammal. 30 (4): 391-392.

Blauvelt, H. 1955. Dynamics of the mother-newborn relationship in goats. p. 221-258. Group Processes. Trans. First Conf. 1954. Josiah Macy Jr. Foundation. B. Schaffner (ed.) New York.

Blauvelt, H. 1956. Neonate-mother relationship in goat and man. p. 94-140. Group Processes. Trans. Second Conf. 1955. Josiah Macey Jr. Foundation. B. Schaffner, (ed.) New York.

Brownlee, A. 1950. Studies in the behaviour of domestic cattle in Britain. Bull. Anim. Behav. 1 (8): 11-20.

Bourlière, F. 1960. The Natural History of Mammals. transl. by H. M. Parshley. A. A. Knopf. New York, 364 p.

Carpenter, C. R. 1934. A field study of the behavior and social relations of howling monkeys. Comp. Psychol. Monogr. 10 (2): 168 p. Johns Hopkins Press. Baltimore, Md.

Corbett, J. L. 1953. Grazing behaviour in New Zealand. Br. J. Anim. Behav. 1 (2): 67-71.

Darling, F. F. 1937. A herd of red deer. Oxford Univ. Press 215 p.

Deakin, A., G. W. Muir and A. G. Smith. 1935. Hybridization of domestic cattle, bison and yak. Canada Dept. of Agric. Technical Bull. 2, 30 p.

De Vos, A. 1960. Behavior of Barren Ground caribou on their calving grounds. J. Wildl. Mgmt. 24 (3): 250-258.

Fraser, A. F. 1957. The disposition of the bull. Br. J. Anim. Behav. 5(3): 110-115.

Fuller, W. A. 1959. The horns and teeth as indicators of age in bison. J. Wildl. Mgmt. 23(3): 342-344.

Fuller, W. A. 1960. Behaviour and social organization of the wild bison of Wood Buffalo National Park, Canada. Arctic. 13 (1): 3-19.

Fuller, W. A. 1962. The biology and management of the bison of Wood Buffalo National Park. Canadian Wildlife Service. Wildl. Mgmt. Bull. Series 1, 16, 52 p.

Garretson, M. S. 1938. The American bison. New York Zool. Soc., New York. 254 p.

Glover, R. 1947. The wisent or European bison. J. Mammal. 28 (4): 333-342.

Harlow, H. F. and R. R. Zimmermann. 1959. Affectional responses in the infant monkey. Science 130 (3373): 421-432.

Heck, L. 1954. Animals my adventure. Methuen & Co. Ltd., London. 170 p.

Heck, L. 1956. Der Rothirsch. Verlag Paul Parey, Hamburg und Berlin.

Hediger, H. 1949, Säugetier-Territorien und ihre Markierung. Bijdragen tot de Dierkunde 28: 172-184.

Innis, A. C. 1958. The behaviour of the giraffe, Giraffa camelopardalis, in the Eastern Transvaal. Proc. Zool. Soc. Lond. 131 (2): 245-278.

Jaczewski, Z. 1958. Reproduction of the European bison, Bison bonasus, in reserves. Acta Theriologica 1 (9):334-376.

Kerruish, B. M. 1955. The effect of sexual stimulation prior to service on the behaviour and conception rate of bulls. Br. J. Anim. Behav. 3 (3): 125-130.

Knaus, W. 1960. Das Gamswild. Verlag Paul Parey, Hamburg and Berlin. 188 p.

Kraft, H. L. 1957. Das Verhalten von Muttertier und Neugeborenen bei Cameliden. Säugetierk. Mitt. 5 (4): 174-175.

Lang, E.M. 1955. Beobachtungen während zweier Giraffengeburten. Säugetierk. Mitt. 3 (1): 1-5.

McHugh, T. 1958. Social behavior of the American buffalo (Bison bison bison). Zoologica 43 (1): 1-40.

Meyer-Holzapfel, M. 1956. Das Spiel bei Säugetieren. Kukenthal's Handbuch der Zoologie, 8 (10).

Mohr, E. 1952. Der Wisent. Die Neue Brehm-Bucherei. Akademische Verlagsgesellschaft Geest & Portig K.-G. Leipzig. 75 p.

Murie, O. J. 1954. A field guide to animal tracks. Houghton Mifflin Co. Boston. 374 p.

Raesfeld, F. von 1957. Das Rotwild. Verlag Paul Parey, Hamburg und Berlin. 384 p.

Roe, F. G. 1951. The North American buffalo. Univ. of Toronto Press. 957 p.

Schein, M. W. and M. H. Fohrman. 1955. Social dominance relationships in a herd of dairy cattle. Br. J. Anim. Behav. 3 (2): 45-55.

Schloeth, R. 1958a. Über die Mutter-Kind-Beziehungen beim halbwilden Camargue-Rind. Säugetierk. Mitt. 6 (4): 145-150.

Schloeth, R. 1958b. Cycle annuel et comportement social du taureau de Camargue. Mammalia 21 (1): 121-139.

Schloeth, R. 1961. Das Sozialleben des Camargue-Rindes. Z. Tierpsychol. 18 (5): 574-627.

Soper, J. D. 1941. History, range and home life of the northern bison. Ecol. Monogr. 11: 347-412.

Thomas, E. 1956. Zur Euter-Suche junger Huftiere. Säugetierk. Mitt. 4 (1): 31.

Walker, D. M. 1950. Observations on behaviour in young calves. Bull. Anim. Behav. 1 (8): 5-10.

Wardrop, J. C. 1953. Studies in the behaviour of dairy cows at pasture. Br. J. Anim. Behav. 1 (1): 23-31.

Woodbury, A. M. 1941. Changing the hook order in cows. Ecology 22 (4): 410-411.

Yermaloff, A. 1906. The bisons of the Caucasus. Ann. Rept. Smithsonian Inst.

B29806